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Bulletin of the British Museum (Natural History)

Anatomy and phylogeny of the Chinese Major Carps *Ctenopharyngodon Steind.*, 1866 and *Hypophthalmichthys* Blkr., 1860

Gordon Howes

Zoology series Vol 41 No 1 27 August 1981

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Anatomy and phylogeny of the Chinese Major Carps *Ctenopharyngodon Steind.*, 1866 and *Hypophthalmichthys* Blkr., 1860

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Synopsis

The Chinese major carps, *Ctenopharyngodon* and *Hypophthalmichthys,* long held to belong to the subfamily Leuciscinae are each shown to represent separate lineages of a diphyletic Cyprinidae. This result is based on the analysis of 22 character complexes and the identification of supposed apomorphies. *Ctenopharyngodon* forms part of a monophyletic assembly termed the *squaliobarbine group* and *Hypophthalmichthys* is identified as the most derived member of the *abramine group*. The squaliobarbines are considered to be the sister group of all other barbelled Cyprinidae. The incongruity of character sets results in the presentation of two hypotheses for abramine intrarelationships. *Hypophthalmichthys* possesses a unique form of epibranchial organ; derived epibranchial structures are also identified in *Xenocypris* and *Abramis.* In the light of the data presented, the classification of the subfamily Leuciscinae is evaluated and many identifications of 'intergeneric' hybrids are falsified. Some comment is made concerning the phylogeny of barbelled cyprinids.

Introduction

The subjects of this study are the Chinese major carps, *Ctenopharyngodon* (the grass carp or white-amure) and *Hypophthalmichthys* (the silver and big-head carps). The object is to put forward a hypothesis of relationships of these taxa based on synapomorphic characters.

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The major Chinese carps are of considerable economic importance as sources of protein and, in the case of *Ctenopharyngodon*, a control agent in restricting pond and canal weed growth. That these carps are primary-consumers and breed well in captivity are additional assets in their culture. Although there is much information on their biology–breeding, physiology, biochemistry and culturing, there are very few papers describing their anatomy. Of these only two or three authors have made statements regarding possible phylogenetic relationships.

Ctenopharyngodon is a monotypic genus included by Chu (1935) in the subfamily Leuciscinae. Berg (1949) considered the genus to be closely related to *Scardinius* and placed it in his all-embracing Cyprinini. Gosline (1978) placed *Ctenopharyngodon, Mylopharyngodon* and *Squaliobarbus* together, and although he was undecided whether they belonged to the subfamily Cyprininae or Leuciscinae, favoured retention in the latter. Even though the characters Gosline used for uniting these genera are considered by the present author to be a mosaic of plesio- and apomorphies, his hypothesis of relationships is not refuted in this study.

Hypophthalmichthys includes three nominal species, *H. molitrix* (Val.), *H. nobilis* (Richardson) and *H. harmandi* Sauvage. Oshima (1919) established the genus *Aristichthys* to contain *nobilis*, believing that differences in gill-raker form, abdominal keel length and pharyngeal dentition from those in *molitrix* were large enough to signify generic rank. Authors have been at variance in treating *Aristichthys* as a valid genus and many still regard *nobilis* as a species of *Hypophthalmichthys.* I would agree with the latter view. The taxa *molitrix* and *nobilis* possess unique synapomorphies and thus belong to the same higher category, ie. the genus *Hypophthalmichthys.* The species *H. harmandi* appears to have been overlooked by subsequent authors. To my knowledge it is known only from the type specimen from Hanoi, now in the Paris Museum.

Günther (1868) first introduced the category Hypophthalmichthina to contain *Hypophthalmichthys* which taxon Gill (1893) later recognized as a subfamily, the Hypophthalmichthinae. Regan (1911; 1922) thought *Hypophthalmichthys* to be related to *Barilius*—a suggestion refuted by Howes (1980). Kryzanovskij (1947) referred *Hypophthalmichthys* to the Leuciscinae on evidence derived from ontogenetic development. Ryabov (1973) agreed with this subfamilial placement, using as his evidence the viability of larvae produced by cross-breeding *Hypophthalmichthys* and *Abramis*—*Abramis* being considered a typical leuciscine. Gosline (1978), relying on a tri-lobed swimbladder as an indicator of this relationship, considered that there were 'clear indications of a cultrin derivation for *Hypophthalmichthys* and *Aristichthys*'. A tri-lobed swimbladder, however, has such a mosaic distribution throughout the Cyprinidae that it has no value as a character indicating shared common ancestry. Besides which, the third 'lobe' in *Hypophthalmichthys* is a mere constriction or 'tail' of the swimbladder and is variously developed in individual fish.

There has been only one study of the comparative osteology of the major Chinese Carps, that by Watanabe (1951). Although this author pointed out significant differences between *Ctenopharyngodon, Hypophthalmichthys* and *Mylopharyngodon,* and noted the possible taxonomic value of certain characters, he made no attempt to utilize them in formulating relationships.

Finally, it can be noted that artificial hybridization between *Ctenopharyngodon* and *Hypophthalmichthys* has been achieved and the morphology of the hybrids described by Berry & Low (1970).

The consensus of ichthyological opinion it would seem, is that the two major carps, *Ctenopharyngodon* and *Hypophthalmichthys* belong to the same subfamily, the Leuciscinae. My thesis is that they do not, but that each represents a distinct monophyletic lineage. representative of a basic dichotomus division within the Cyprinidae.

Abbreviations used in the figures

AA	Anguloarticular	Aap	*Adductor arcus palantini* muscle
AEW	Anterior wall of epibranchial organ	Ah	*Adductor hyomandibularis* muscle

AMP	Anterior medial maxillary process
BO	Basioccipital
BOCB	Basioccipital cartilaginous bloc
BOK	Basioccipital keel
BON	Basioccipital notch
BP	Basioccipital pharyngeal process
BUC	Buccal cavity
CB	Ceratobranchial (numbered)
CF	Ceratobranchial filaments
CFE	Carotid fenestra
CP	Coronoid process
CPE	Cartilaginous preethmoid
Dahm	Dorsal section of *adductor hyomandibularis*
DPTC	Dermopterotic canal
EB	Epibranchial (numbered)
EBD	Epibranchial duct (numbered)
EBO	Epibranchial organ
EC	Ethmoid cartilage
ECT	Epibranchial connective tissue
EOD	Epibranchial oesaphagal duct
EOW	Epioccipital wing
EP	Epioccipital
EPOP	Epioccipital process
ER	Epibranchial rakers
ES	Extrascapular
EXO	Exoccipital
EXOF	Exoccipital flange
F	Frontal
FC	Frontal canal
FF	Frontal foramen
FIC	Internal carotid foramen
FJ	Jugular foramen
FII	Optic foramen
FV	Foramen for trigeminal trunk
FVII	Foramen for facial nerve trunk
FVIII	Foramen for acoustic nerve
FIX	Foramen for glossopharyngeal
GR	Gill raker (globular)
HMF	Hyomandibular fossa
HYO	Hyomandibular
HVII	Hyomandibular branch of VII nerve
IC	Intercalar
ICF	Intercalar fossa
IF	Infrapharyngobranchials (numbered)
IO	Infraorbitals (numbered)
IOP	Interoperculum
LE	Lateral ethmoid
LEF	Lateral ethmoid/frontal fenestra
LEN	Supraethmoid notch for palatine head
LOF	Lateral occipital foramen
ME	Mesethmoid
MET	Metapterygoid
MF	Maxillary foramen
MMP	Midlateral maxillary process
MP	Masticatory plate
N	Nasal
NC	Neural complex
NS	Neural spine
OC	Intramural opercular canal
OFT	Olfactory foramen
OP	Operculum
OPE	Ossified preethmoid
PALH	Palatine head
PAR	Parietal
PE	Preethmoid
PEW	Posterior wall of epibranchial organ
PF	Palatal fold
PFO	Prootic foramen
PH	Pharyngeal bone
PHF	Fossa in pharyngeal bone
Php	Pharyngeal pad
PO	Preoperculum
POC	Preopercular canal
PPSF	Prootic/paraspenoid fenestra
PRO	Prootic
PS	Parasphenoid
PSAP	Parasphenoid ascending process
PSCB	Parasphenoid keel
PTE	Pterotic
PTES	Pterotic spine
PTS	Pterosphenoid
PTT	Posttemporal
PVP	Pterosphenoid ventral process
Q	Quadrate
SE	Supraethmoid
SEW	Supraethmoid wing
SM	Ceratobranchial sifting membrane
SO	Supraoccipital
SOCC	Supraoccipital crest
SOP	Subopercle
SOR	Supraorbital
SP	Sphenotic
V	Vomer
Vahm	Ventral section of *adductor hyomandibularis* muscle
VPSR	Ventral parasphenoid ridge

Study material

All specimens used in the preparation of this paper are in the osteological and alcohol collections of the British Museum (Natural History). Lists of comparative material will be found in previous publications (Howes, 1978; 1979). The catalogue numbers for specimens used in illustrating this work are given in the figure captions.

Comparison of selected characters in *Ctenopharyngodon* and *Hypophthalmichthys*

The following 22 characters were selected after a preliminary study had eliminated others which appeared to contain minimal information concerning their plesio- or apomorphic state (ie. intra- and interspecifically variable or mosaically distributed), and those which were considered to be symplesiomorphies. Guidance to the identification of plesiomorphic character state came both from previous studies on cyprinid phylogeny (Howes, 1978; 1979; 1980) and wider outgroup comparisons—outgroup in this case being other otophysans. Likewise, these earlier studies had led to the final selection of those characters which had previously been useful as phylogenetic indicators. Reasons for polarity assignment are present in the analysis below.

Selected characters: 1. Ethmo-vomerine region; 2. Pterosphenoid; 3. Parasphenoid; 4. Prootic; 5. Subtemporal fossa and associated musculature; 6. Dilatator fossa; 7. Frontal; 8. Parietal; 9. Circumorbitals; 10. Supraoccipital; 11. Exoccipital; 12. Epioccipital; 13. Intercalar; 14. Basioccipital; 15. Posttemporal; 16. Opercular series; 17. Suspensorium; 18. Jaws; 19. Vertebral column; 20. Gill-arches; 21. *Adductor hyomandibulae* muscle; 22. Pectoral girdle.

Analysis of apomorph characters

1. *Ethmo-vomerine region*

Ctenopharyngodon (Fig. 1); supraethmoid broad and short with a shallow medial anterior notch and two lateral notches; preethmoids paired, largely cartilaginous; kinethmoid dorsally expanded; vomer widely V-shaped anteriorly; lateral ethmoid wall truncate.

Hypophthalmichthys (Fig. 1); supraethmoid broad and short with a deep medial notch; preethmoid single, small, completely ossified; kinethmoid rod-shaped; vomer thickened anteriorly and forming the floor of the median ethmoid notch; lateral ethmoid contains entire olfactory foramen in a bony tube; the lateral lamella is prolonged distally and curves ventrally; fenestra between the dorsal surface of the lateral wall and the frontal.

Both *Ctenopharyngodon* and *Hypophthalmichthys* possess a short, broad *supraethmoid* and depressed *mesethmoid.* This is hypothesized as the plesiomorph condition in cyprinids on the grounds of widespread occurrence. Within the Cyprinidae there are two basic forms of supraethmoid; (1) in which the anterior border of the bone is indented medially so as to accommodate the retracted kinethmoid (sometimes there may be indentations lateral to the medial one), and (2) where the supraethmoid is rostrally extended, its lateral border rounded and the tip of the extension bearing the median notch. These two types are illustrated in Fig. 2.

The first morphotype is that most commonly encountered in non-barbelled Cyprinidae (ie. Leuciscinae), whilst the second is that found in almost all barbelled Cyprinidae (ie. Cyprininae; *Barbus, Labeo* etc). In *Cyprinus, Carassius* and several members of the Gobioninae, although there is a prominent rostral process there is no, or but a slight, medial notch—the kinethmoid being attached to the base of the rostral process by a single ligament (oberes Rüsselband of Fiebiger, 1931). This is similar to the condition in the Catostomidae where the supraethmoid is elongate and without a medial indentation.

A rostrally produced supraethmoid is the common condition amongst characoids and a comparison between the ethmoid region of *Brycon* and that of *Catostomus* shows a remarkable similarity. In siluroids the common condition, as in cyprinoids, appears to be one where the anterior ethmoid border bears a slight medial indentation. Within the cyprinids, although the extremes of the two ethmoid morphotypes can be readily appreciated, they are linked by a series of intergrades. Particular examples are in *Garra*

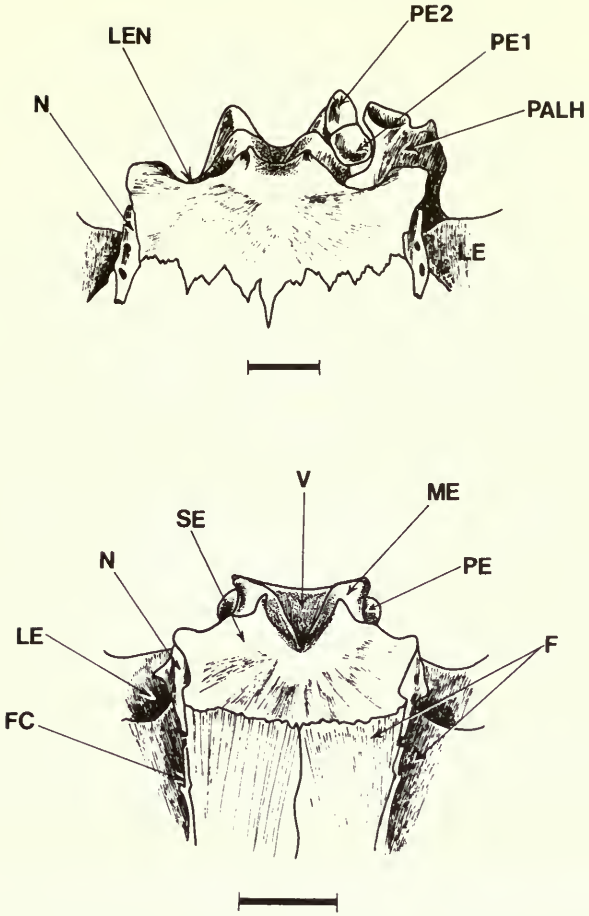


Fig. 1 Ethmo-vomerine regions in dorsal view: (upper) *Ctenopharyngodon idellus*; (lower) *Hypophthalmichthys molitrix*. Specimens BMNH 1888.5.15 : 25; 1895.5.31 : 22. Scales = 10 mm.

where the rostrally produced ethmoid shape is still discernible but the anterior border is deeply indented as in 'leuciscines'. Again, in some species of *Barbus* and *Schizothorax* the ethmoid is distinctly leuciscine-like. An extreme morphotype is encountered in *Semiplotus* and *Scaphiodonichthys* where the entire supraethmoid is almost vertically directed and it is the anterior border of the frontal which is medially indented. In general, it appears that cyprinids with a terminally placed mouth are those with a deeply notched ethmoid. On the other hand, the rostrally produced ethmoid is more characteristic of bottom feeding types where additional, almost ventral extension of the mouth is functionally desirable—as in *Semiplotus* mentioned above. Fink & Fink (1981) propose that a rostrally produced ethmoid is plesiomorphic for otophysans. It would appear that in cyprinids a supraethmoid with a slight, but broad rostral process is the plesiomorph state. This plan would offer the potential of producing either kind of morphotype. The variability of the supraethmoid in species of *Barbus* is discussed by Banister (in preparation). In that group, at least, the ethmoid appears to be a very labile structure and one responding to environmental influences.

In *Ctenopharyngodon* there are lateral indentations on either side of the medial supraethmoid notch (LEN, Fig. 1). These lateral notches accommodate the enlarged anterior condyles of the palatines. A similar feature occurs in *Squaliobarbus* and *Mylopharyngodon* and is considered synapomorphic.

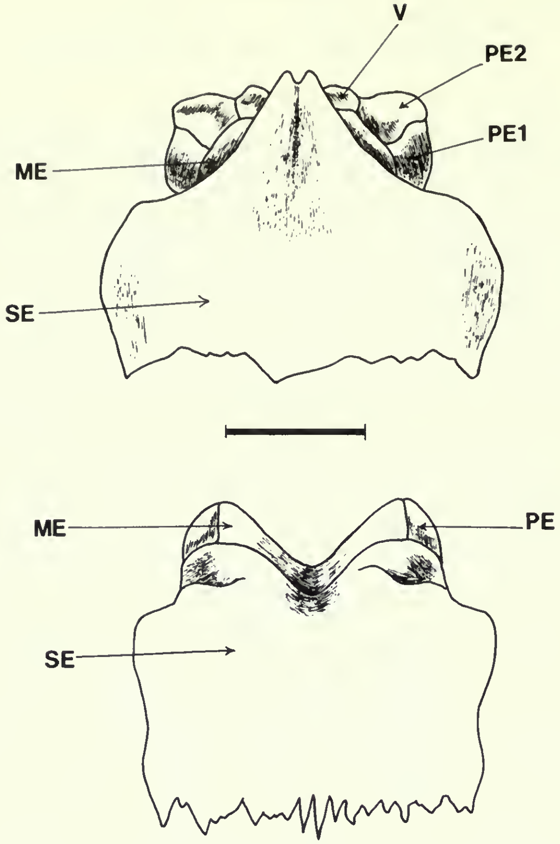


Fig. 2. Ethmo-vomerine regions in dorsal view: (upper) *Cyprinus carpio*; (lower) *Leuciscus cephalus*. Composite drawing of several specimens. Scale = 5 mm.

Concerning the posterior border of the supraethmoid, a transverse suture with the frontal appears to be the plesiomorph state. Only in some chelines is the posterior margin rounded or triangular and overlapped by the frontals (see Ramaswami, 1955*b*, fig. 3, and Howes, 1979). Amongst characoids the posterior ethmoid margin is triangular, that of siluroids is irregular, its medial part usually invaded by the anterior tip of the frontal fontanel.

A rod-shaped *kinethmoid* is considered the plesiomorph type (see Howes, 1978). I am unaware of any detailed study concerning the possible derivation or homology of the bone. Goodrich (1909) thought it to be a specialized part of the ethmoid. The common occurrence of a bifurcated kinethmoid suggests that there has been a phylogenetic ossification into a single unit of two premaxillary-ethmoid ligaments. There is no cyprinoid known to me in which these ligaments remain unossified in the adult, or even in larval stages, and which would represent the most plesiomorph state. In its various derived states the dorsal part of the kinethmoid may be expanded in a transverse plane, or the medial part of the bone may be swollen.

In *Ctenopharyngodon* the kinethmoid is dorsally expanded and thickened, a derived condition encountered in other cyprinid groups (eg. chelines; see Howes, 1979). In *Hypophthalmichthys* the bone remains as a slender rod.

Ramaswami (1955*a*) noted the absence of a *preethmoid* in *Hypophthalmichthys*, but this is not the case. A preethmoid cartilage is present, although minute and only fully ossified in the adult. Likewise, in other genera which Ramaswami (1955*a* & *b*) cites as lacking a preethmoid, I have found it as a poorly ossified element. Ossification of the preethmoid is variable; specimens of *Alburnus* show no sign of ossification until they are at least 56 mm SL;

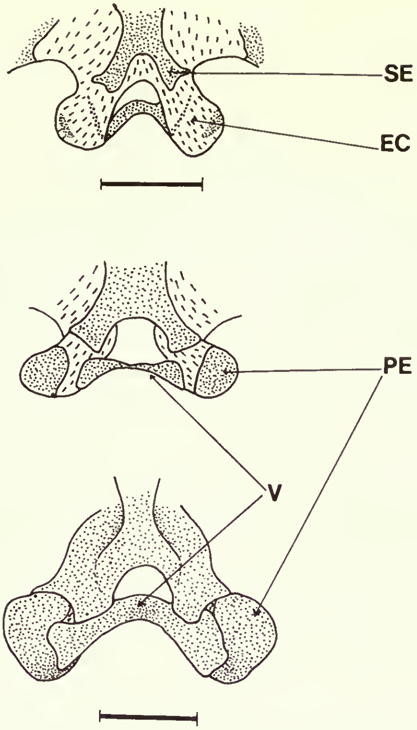


Fig. 3 Development of the ethmoid bloc in *Barbus* sp. Anterior view (top) from a specimen 13 mm SL; (centre) specimen 20 mm SL; (bottom) specimen 35 mm SL. Dashed areas = cartilage, stippled areas = ossification. Scales = 0·5 mm.

the preethmoid in *Oreoleuciscus* is entirely cartilaginous in a specimen of 114 mm SL. It is still recognizable as a preethmoid, being clearly differentiated from the ossified mesethmoidal process.

According to Alexander (1966) the preethmoid is an ossification of the antero-lateral process of the ethmoid cartilage (mesethmoid). He notes that in *Leuciscus* (= *Idus* of Alexander), the maxillary ascending process articulates with the preethmoid cartilage, and with the palatine *via* a cartilaginous insert (submaxillary meniscus of Alexander). Corroboration of Alexander's (1966) statement that the preethmoid is an ossification of the mesethmoid comes from an ontogenetic series of *Barbus* sp. (Fig. 3). In the smallest specimens, 12–14 mm SL, the preethmoid is not differentiated from the ethmoid cartilage and there is a sub-terminal ossification, in 20 mm specimens there is dorsal ossification of the lateral mesethmoid processes, greater area of terminal ossification and antero-lateral extension of the vomer. In specimens of between 25 mm and 27 mm SL there exists only a small area of cartilage between the mesethmoid, ossified preethmoid and vomer. At the 30–35 mm stage, the antero-lateral mesethmoid processes have contacted the now large and completely ossified preethmoids and the vomer. A lateral mesethmoid-vomerine fossa is formed and the preethmoid contacts the fossa *via* a thin meniscus of cartilage.

In all cyprinids I have examined, other than abramines (see below), the preethmoid is contained in a lateral fossa formed from the mesethmoid and the vomer (see Howes, 1978).

A lateral ethmo-vomerine fossa is lacking in *Abramis, Rutilus, Chondrostoma* and *Xenocypris.* In these taxa the vomer does not protrude laterally (see below) but extends forward; the preethmoid is extensive and covers the extended vomerine arm, contacting the mesethmoid only along its antero-ventral rim (see Figs 5A–D). The preethmoid is almost entirely cartilaginous with only the anterior tip being ossified in the case of *Abramis, Rutilus*

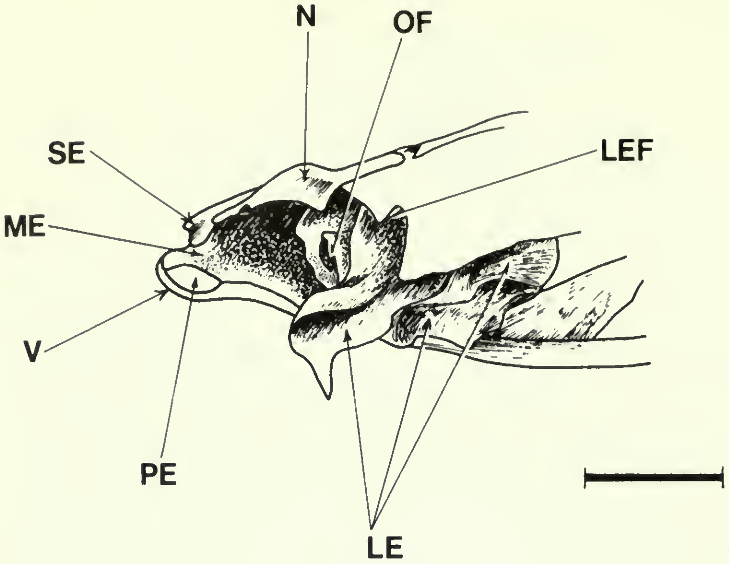


Fig. 4 *Hypophthalmichthys molitrix,* lateral view of ethmo-vomerine region. Specimen 1895.5.31 : 22. Scale = 10 mm.

and *Chondrostoma,* but a laterally ossified nub in *Xenocypris.* Although in *Hypophthalmichthys* there is a distinct reduction of the lateral fossa the preethmoid cartilage still contacts the lateral part of the mesethmoid (Fig. 4). Laterally, the preethmoid articulates directly with the palatine facet; only rarely is such a connection lacking (eg. *Ochetobius*); there is never direct contact with the maxilla. In some cyprinids, however, the preethmoid is extended anteriorly and may ossify into two parts. Such paired preethmoids were recorded in *Cyprinus* by Fiebiger (1931) as the lateral 'seitliches Knötchen' articulating with the palatine, and the anterior 'Sesamknöten' articulating with the maxilla. Paired preethmoids also occur in *Ctenopharyngodon* (Fig. 1), *Mylopharyngodon, Squaliobarbus* and some *Barbus* species. In these taxa, the anterior preethmoid is often unossified or only partially so. According to Ramaswami (1955*a*) it is the cartilage sandwiched between the maxilla and the preethmoid which ossifies to form a second preethmoid. However, in the taxa cited above, the additional, anterior ossification would appear to be within the original preethmoidal cartilage.

In gobioinids, cobitids and catostomids, the second preethmoid can be exceptionally well-developed and exists as an ossified strut (the septomaxilla of Regan, 1911 and Starks, 1926). Patterson (1975 : 501) reckons the preethmoids of cyprinoids to be neomorphs. As such they must be regarded as autapomorphic for Cyprinoidei. A single, lateral ossification of the ethmoid cartilage articulating with the palatine is hypothesized as representing the plesiomorph condition (see Howes, 1980).

The *mesethmoid* is usually a triangular bloc, its apex forming the rostrum of the entire ethmoid bloc. In those taxa with a medially indented supraethmoid, the mesethmoid becomes thickened anteriorly and forms a somewhat hour-glass shape. In some leuciscines, the mesethmoid is laterally excavated to such an extent that it is virtually a medial septum. The posterior wall of the mesethmoid cartilage is, in one group of leuciscines and some cyprinines, excavated to form the anterior myodome (see below).

The *lateral ethmoid* in cyprinids most often has a well-produced lateral wall with a broadly-triangular base; antero-medially it meets the mesethmoid and contains part of the olfactory nerve foramen in its leading edge; postero-medially it meets its fellow along the midline. In some cases the lateral ethmoids are indented into the mesethmoid cartilage so as to form an *anterior myodome.* Even though, as in aspinines, the anterior myodome extends

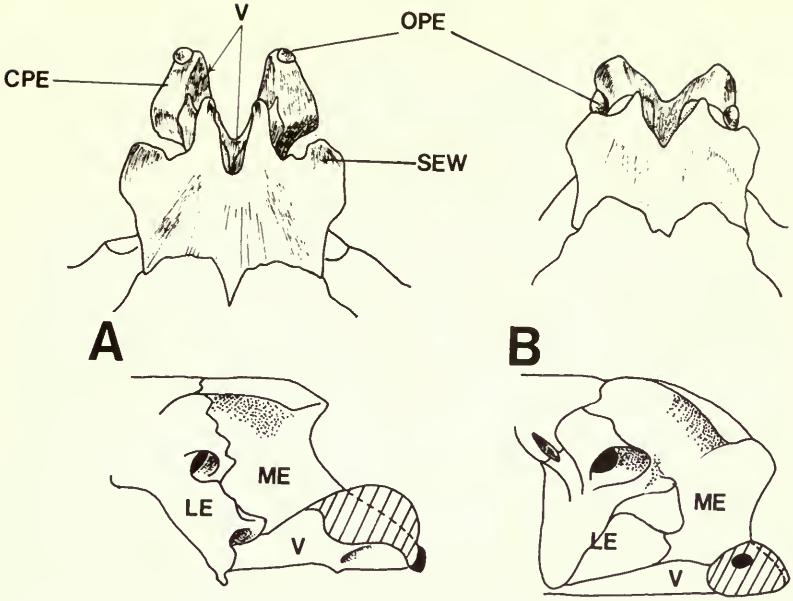


Fig. 5 Ethmo-vomerine regions in dorsal and lateral views: A. *Abramis brama*; B. *Xenocypris argenteus*. The lateral views are semi-diagrammatic and show the anterior edge of the vomer as a dashed line, the cartilaginous preethmoid as cross-hatched and the ossified preethmoid as black. Composites, from skeletal and alizarin specimens; all drawn to same scale.

well forward, the lateral ethmoids remain in medial contact. However, in *Barbus barbus, Cyprinus* and *Carassius,* the myodome invades the mesethmoid cartilage through a parting between the lateral ethmoids. Patterson (1975) was unable to conclude whether the absence of an anterior myodome was a primitive condition or due to secondary loss (apomorphic). Its presence does not seem necessarily to be correlated with any particular degree of ethmoidal elongation, nor its absence with any shortening. In noemacheilids, gobioinids and catostomids, an anterior myodome is lacking. Widespread, mosaic distribution in cyprinids and almost universal presence in characoids probably indicates that an anterior myodome is a plesiomorph feature.

In *Ctenopharyngodon* and *Mylopharyngodon* the olfactory foramen is entirely countersunk within the lateral ethmoid, whereas in *Hypophthalmichthys* it projects forward as a bony tube (Fig. 4). In the latter genus there is a tubular opening between the medial dorsal part of the lateral ethmoid wall and the overlying frontal (LEF, Fig. 4). This tube contains a thick ligament which covers the top of the lateral ethmoid wall and the outer part of the supraorbital. A similar feature occurs in *Xenocypris* (Fig. 5B). In cyprinids the olfactory foramen is most often formed from the anterior margin of the mesethmoid. In some taxa, however, the foramen is confined entirely within the lateral ethmoid. This occurs in the taxa cited above, in alburnine genera (*Alburnus, Chalcalburnus*) and some *Barbus.* In *Barbus tropidolepis* the foramen is also housed in an anteriorly projecting tube (Banister, pers. comm.). On the basis of other sets of synapomorphic characters it is hypothesized that the occurrence of a tubular olfactory foramen in diverse taxa is of no phyletic significance.

A short and broad *vomer* is hypothesized as plesiomorphic eg. as in *Ctenopharyngodon* and *Hypophthalmichthys.* However, in *Hypophthalmichthys* the vomer extends anteriorly to floor the median ethmoid notch, its anterior margin is almost straight and is curved upward so as to face the lower part of the ethmoid bloc. Laterally, the vomer is indented to contain the preethmoid. An anteriorly extended vomer, flooring the median ethmoid notch is a rarely encountered feature amongst cyprinids. In some cultrines (*Culter*) and in *Ochetobius* (currently included in the Leuciscinae), the vomer forms the floor of a shallow but wide

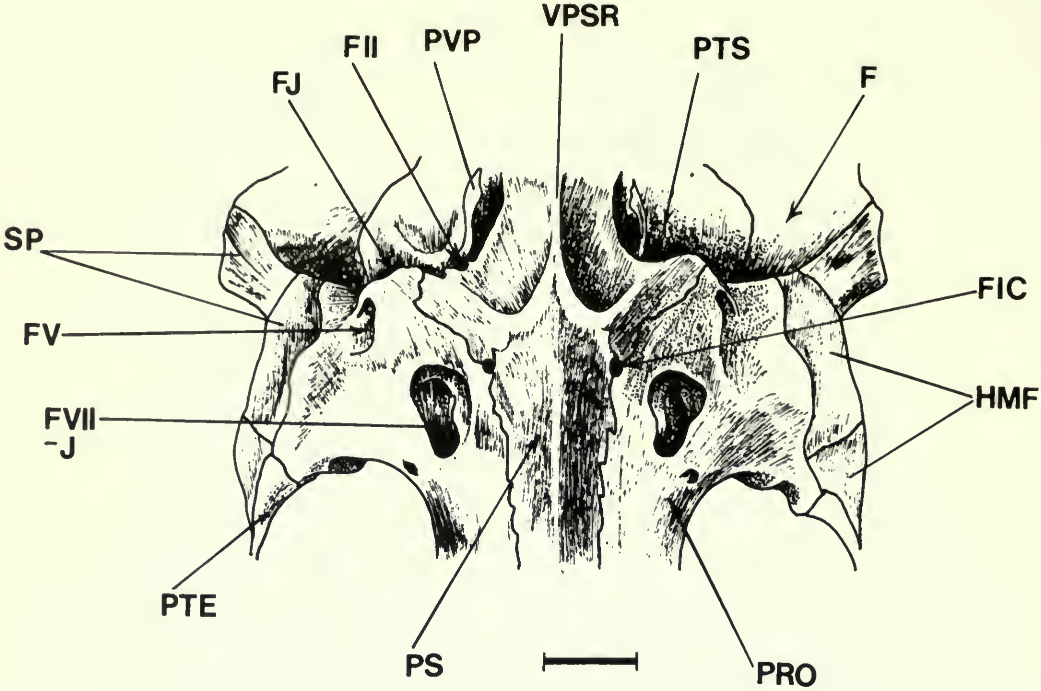


Fig. 6 *Ctenopharyngodon idellus,* ventral view of anterior otic region. Specimen BMNH 1888.5.15 : 25. Scale = 10 mm.

ethmoid notch. In *Xenocypris* and *Abramis,* the vomer also floors the ethmoid notch but the mesethmoidal walls are deep, almost meeting one another ventrally and leaving only a narrow area of the vomerine floor visible from above (Figs 5A & B). As mentioned above (p. 7) *Xenocypris, Abramis, Chondrostoma* and *Rutilus* differ from other cyprinids in employing the vomer as the platform for the preethmoid and excluding the mesethmoid from taking part in its support. In these genera the vomer is deeply forked, each arm extending some distance anteriorly from the mesethmoidal border; in transverse plane the bone is markedly convex.

2. *Pterosphenoid*

Ctenopharyngodon (Fig. 6); contact between the pterosphenoid and ascending process of the parasphenoid is *via* a thin strut; medial contact with the prootic is by a long suture. On the lateral face of the pterosphenoid is a small, ventrally directed process (autapomorphic feature; PVP, Fig. 6).

Hypophthalmichthys (Fig. 7); contact with the parasphenoid is *via* a thick, anteriorly directed pillar-like process. The part to the anterior trigemino-facialis foramen, and a medial portion of the bone provides the inner wall of the anterior part of the chamber; this is a unique condition in cyprinids.

Howes (1979) presented a classification of the various types of contact between the parasphenoid and pterosphenoid, assuming that this classification reflected a phylogenetic sequence for the Cyprinidae as a whole. Further analysis has shown that similar sequential series can be detected in all groups so far identified as monophyletic, ie. the plesiomorphic condition is one with no contact between para- and pterosphenoid (Type 1 and derived Type 1 in Howes, 1980) and the most apomorphic condition involves extensive lateral contact between the pterosphenoid and parasphenoid (Type 5 in Howes, 1980).

A pterosphenoid pedicle is present in various teleosts and may or may not contact the

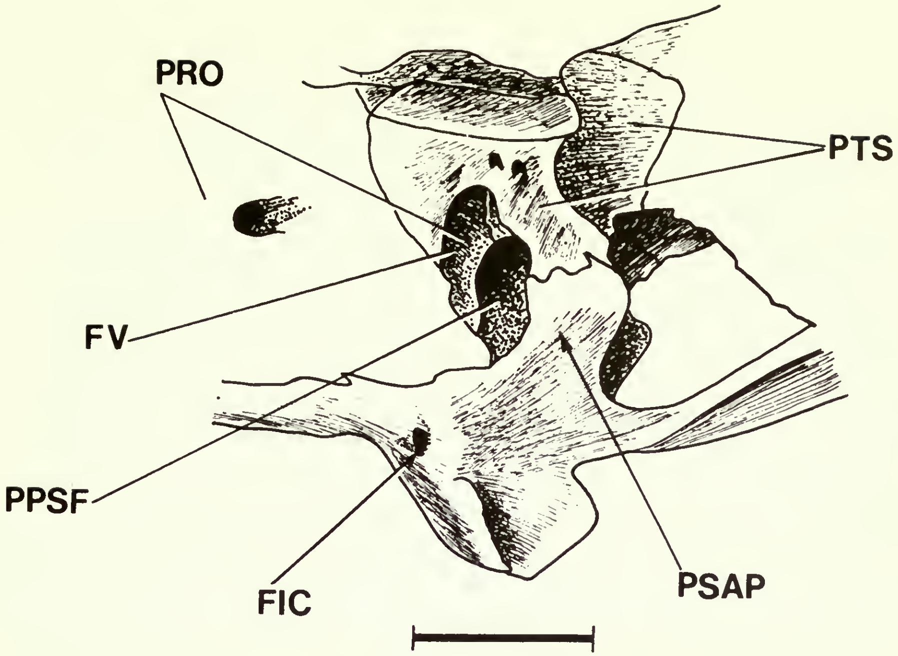


Fig. 7 *Hypophthalmichthys molitrix,* lateral aspect of anterior otic region, viewed slightly antero-ventrally. Drawn from specimen BMNH 1895.5.31 : 22 with additions from alizarin preparations and dissections from BMNH 1980.5.21 : 5–14. Scale = 10 mm.

parasphenoid ascending process. Patterson (1975) regards this feature as a plesiomorphic one.

3. *Parasphenoid*

In both *Ctenopharyngodon* and *Hypophthalmichthys* the parasphenoid is anteriorly broad, narrowing posteriorly in *Hypophthalmichthys* but remaining broad in *Ctenopharyngodon* in which genus it bears a marked ventral medial range. In *Hypophthalmichthys* the hypophyseal portion of the parasphenoid is ventrally extended into a long deep process, or keel the posterior edge of which is developed into a transverse ridge. The ventral keel serves both as the anterior point of attachment for a medial cartilaginous insert dividing the forward part of epibranchial diverticula (p. 23) and as lateral sites of attachment for the *adductor arcus palatini* muscle (p. 37).

In the majority of cyprinids the central surface of the parasphenoid is grooved, rarely is there a midline ridge or process, and these features are regarded as derived. The anterior broadening of the parasphenoid, although extreme in the Chinese major carps, is a common feature in cyprinids (see Ramaswami, 1955*b*). Weisel (1960) notes that in *Catostomus* the anterior part of the parasphenoid is considerably wider than that of cyprinids. However, this is not so when compared with the two taxa discussed here.

Ctenopharyngodon shares with *Mylopharyngodon* the developed ventral midline ridge and deep anterior concavity of the parasphenoid, both features regarded as apomorphic. The hypophyseal keel of *Hypophthalmichthys* is a feature shared with *Xenocypris* and *Abramis,* although in these taxa it is developed to a lesser extent (see below).

The *internal carotid fenestra* in *Ctenopharyngodon* is small and indents the posterior border of the parasphenoid ascending process and the antero-ventral margin of the prootic. In *Hypopohthalmichthys* the internal carotid artery passes through a small foramen situated in the basal part of the parasphenoid keel (Fig. 7).

Patterson (1975) considered that the plesiomorph condition of the carotid opening in teleosts is for it to occur as a foramen within the parasphenoid. In nearly all cyprinids I have examined, and in all characoids, the internal carotid passes through a fenestra between the parasphenoid and the prootic, a condition Patterson (1975) thought derived and due to the eroding of the parasphenoid ascending process. In catostomids (see Weisel, 1960) and siluroids (?all) the foramen is situated entirely within the parasphenoid. Although similarly there is a parasphenoid carotid foramen in *Hypophthalmichthys* I consider this to be a derived condition in this taxon and for the following reasons.

In *Alburnus, Rutilus, Chondrostoma* and *Abramis,* the internal carotid fenestra is extensive (Fig. 8); it is covered laterally by a fascia of tissue and plugged by a wedge of fat leaving a small ventral opening to allow passage of the carotid vessel. In *Abramis* there is a tendency for the fenestra to elongate and in *Abramis sapa* the 'fenestra' is divided; the lower opening being confined to the parasphenoid and carrying the internal carotid artery, the upper indenting the ventral margin of the prootic and not providing passage for any vessel (Fig. 8). It is hypothesized that the condition of the carotid fenestra in *Abramis sapa* is a derived one and represents a transitional stage toward that in *Hypophthalmichthys.* That this is the directional path and not the reverse, *viz* the incorporation of the foramen into a fenestra, as indicated by the morphology of the parasphenoid. In *Abramis* there is a ventral extension of the hypophyseal part of the parasphenoid similar to that in *Hypophthalmichthys* (see above), and this is most highly developed in *A. sapa* (Fig. 8). Furthermore, the carotid foramen in *Hypophthalmichthys* is situated in the ventral keel, rather than (plesiomorphically) in the ascending process (Patterson, 1975). Similarly, an internal carotid foramen occurs in the same position in *Xenocypris* but is a larger hole than in *Hypophthlamichthys.*

On the basis of this evidence I suggest that the foramen for the internal carotid artery in *Hypophthalmichthys* and *Xenocypris* is secondarily derived in its position in the parasphenoid. This positioning has come about both as a consequence of the ventral prolongation of the parasphenoid and the re-orientation of the first branchial arch (p. 31) whereby the plane of the efferent artery would be sagittal rather than transverse. Thus, this shared feature in *Hypophthalmichthys* and *Xenocypris* is considered a synapomorphic character.

Modifications to the ventral border of the parasphenoid are present in a unit of leuciscine taxa represented by *Abramis, Rutilus* and *Chondrostoma.* In these genera, there is a deep ventral channel in the posterior part of the parasphenoid. The channel is confluent with a similar feature in the basioccipital and the whole is filled with a cartilaginous block (Fig. 27). Discussion of this character is reserved for inclusion with that of the basioccipital (p. 23).

Mention should be made here of medial parasphenoid processes. In *Labeo* and related taxa (see Howes, 1980 : 152, fig. 26 and p. 16 below) a process arises from either side of the medial wall of the parasphenoid just anterior to the optic foramen. Each process contacts the ventral border of each respective pterosphenoid. These medial processes vary from thin struts to thick pillars. Only in *Pelecus* is there a single, medial parasphenoid pillar. These structures are not to be interpreted as homologues of the basisphenoid. Harrington (1955) reported that Holmgren & Stensio (1936) recognized a basisphenoid in some cyprinids, eg. *Abramis.* However, the structure reported by Holmgren & Stensio is the lateral pterosphenoid strut that makes contact with the parasphenoid wing. The medial parasphenoid extensions of *Pelecus* and *Labeo* are considered as neomorphs.

4. *Prootic*

Ctenopharyngodon (Fig. 6); contact with the parasphenoid ascending process is *via* a long suture. The posterior opening of the trigemino-facialis chamber is large and lies ventrally. The upper posterior part of the bone is deeply concave and forms the entire inner face and part of the roof of the subtemporal fossa.

Hypophthalmichthys (Fig. 7); no contact with the parasphenoid ascending process. The posterior trigemino-facialis foramen is small and situated laterally. The upper posterior half

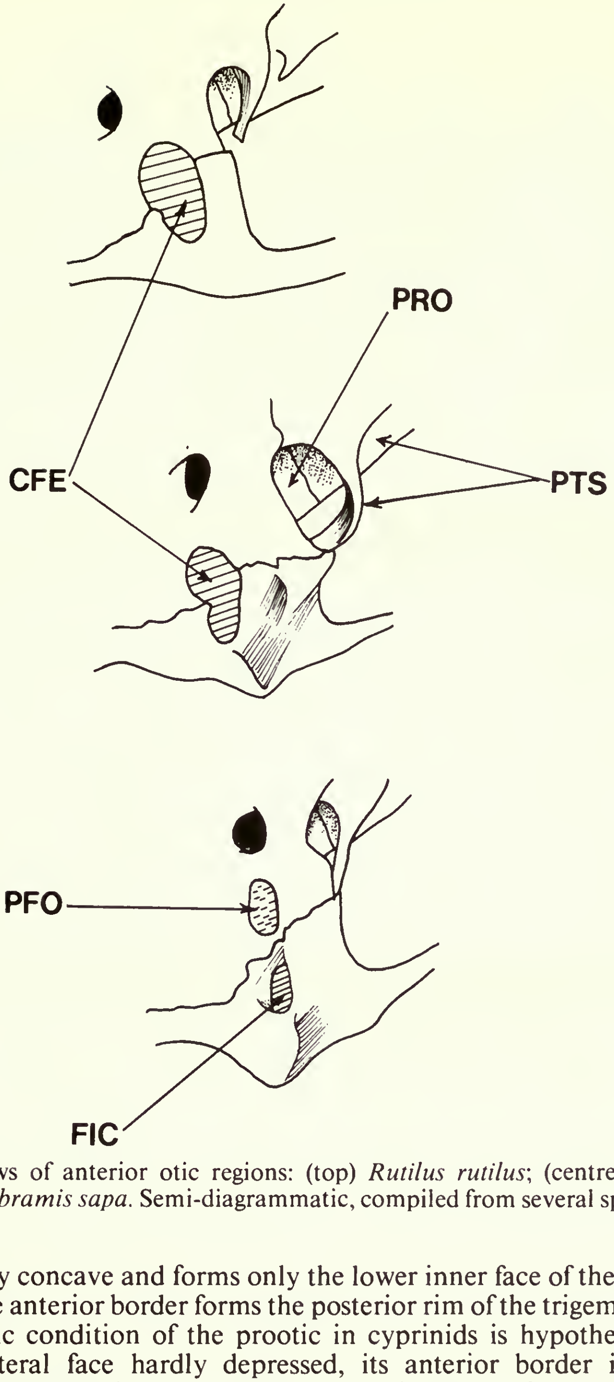


Fig. 8 Lateral views of anterior otic regions: (top) *Rutilus rutilus*; (centre) *Abramis brama*; (bottom) *Abramis sapa*. Semi-diagrammatic, compiled from several specimens.

of the bone is slightly concave and forms only the lower inner face of the subtemporal fossa. The lower part of the anterior border forms the posterior rim of the trigeminal exit fenestra.

The plesiomorphic condition of the prootic in cyprinids is hypothesized as an almost square bone, its lateral face hardly depressed, its anterior border interrupted by the trigeminal exit foramen and with a short lateral commissure (see for example, *Opsariichthys* in Howes, 1980). Derived conditions are those where the anterior trigeminal foramen pierces the lateral face; the lateral commissure is long, and the prootic contributes a ventral portion to the apophyseal platform.

The general depression of the otic part of the cranium in *Ctenopharyngodon* has resulted in the forepart of the prootic being laterally extended (Fig. 6), which, as a consequence, has shifted the orientation of the posterior trigeminal foramen. This opening faces ventrally

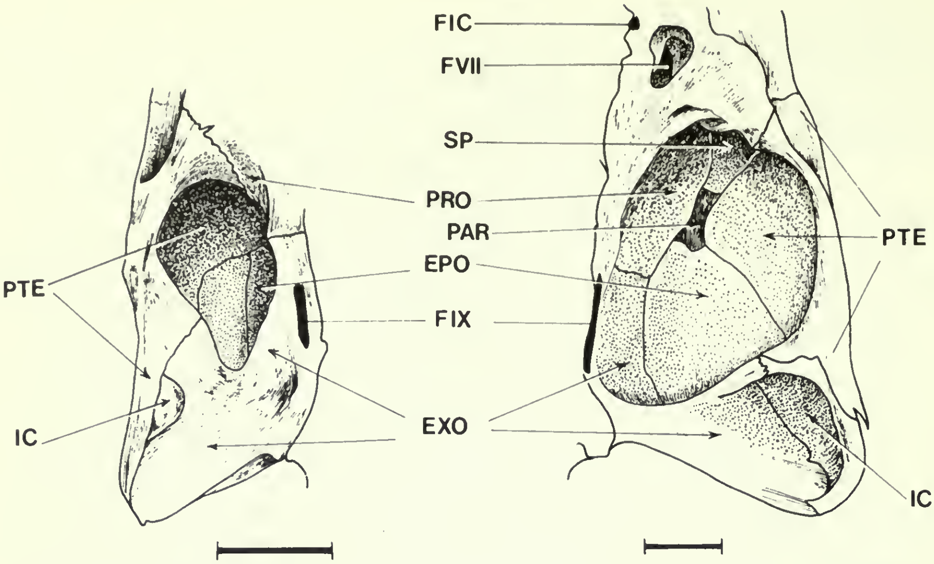


Fig. 9 Subtemporal fossae: (left) *Hypophthalmichthys*; (right) *Ctenopharyngodon*. Specimens BMNH 1888.5.31 : 22 and 1888.5.15 : 25. Scales = 10 mm.

instead of laterally, so the nerve trunk and jugular vein enter without passing across the prootic face. This derived condition occurs also in *Mylopharyngodon* and *Squaliobarbus*.

The most outstanding feature of the prootic in *Hypophthalmichthys* is the exclusion from the bone of the anterior trigeminal foramen. Only the lower part of the prootic forms the border of the opening, the upper part of the foramen being confined to the pterosphenoid. In one specimen, the upper part of the foramen, through which mdV and mxV exit is, on one side of the cranium, entirely enclosed in the pterosphenoid. Reduction of the anterior part of the prootic in *Hypophthalmichthys* appears to have occurred with the posterior movement of the pterosphenoid, itself associated with hypertrophy of the *adductor hyomandibularis* muscle. The form of the prootic in *Hypophthalmichthys* is an autapomorphic feature.

5. *Subtemporal fossa*

Ctenopharyngodon (Fig. 9); extensive, hemiovoid with a deep conical anterior portion, or chamber, that extends into the autosphenotic; the *levator posterior* muscle arising from that bone. The inner wall of the fossa is formed from the prootic, the roof from the pterotic and epioccipital, and anteriorly from the sphenotic. None of these bones meet dorsally and the ventral surface of the parietal is exposed thus also contributing to the subtemporal fossa roof.

Hypophthalmichthys (Fig. 9); almost pyramidal, lacking an anterior sphenotic extension. The posterior, exoccipital border of the fossa is indented by a notch. The bones forming the inner wall of the fossa, prootic, exoccipital and epioccipital, do not meet along their respective dorsal and anterior borders, the space between being a thin cartilage wall.

The most frequently occurring subtemporal fossa morphology amongst the Cyprinidae is one which is deep and circular or ovate. The fossa is the site of origin for *levator posterior* muscles running to the pharyngeal bone and its size is correlated with that of the muscles' size and their orientation. It is thus difficult to assess the polarity of some features such as the posterior notch, which occurs not only in *Hypophthalmichthys* but in a variety of 'leuciscine' and 'barbine' taxa. There is generally a space between the bones forming the inner wall of the subtemporal fossa (*viz* between the posterior-dorsal edge of the prootic, posterior edge of the sphenotic, and antero-dorsal edge of the epioccipital) across which is a thin cartilage and which forms the apex of the fossa. In this feature *Ctenopharyngodon* and *Hypophthalmichthys* are each autapomorphic. In the former taxon the space is covered by the parietal and in the latter taxon the exoccipital contributes substantially to the inner face and its antero-dorsal edge contacts the cartilaginous sheet.

The vast subtemporal fossa of *Ctenopharyngodon* is a feature shared only with *Mylopharyngodon* and *Squaliobarbus*. Likewise, in these two genera the fossa extends anteriorly deep into the sphenotic from which the *levator posterior* musculature originates. The size, shape and sphenotic contribution of the subtemporal fossa in these three genera is considered synapomorphic. The anterior contribution of the sphenotic to the subtemporal fossa occurs also to a greater or lesser degree in *Cyprinus*, *Carassius* and in some *Barbus*, and in the two former taxa part of the *levator posterior* musculature originates in that anterior extension. This may thus represent a synapomorphy linking all these genera (see p. 49).

The shape and depth of the *Hypophthalmichthys* subtemporal fossa are shared with *Xenocypris*. However, these parameters are treated with caution as synapomorphies; variations in subtemporal fossa depth cover a wide range throughout the cyprinids. *Abramis* has what is possibly the deepest subtemporal fossa and again, its pyramidal shape greatly resembles that of *Hypophthalmichthys*. Neither in *Xenocypris* nor *Abramis* does the exoccipital contribute substantially to the inner wall of the subtemporal fossa. Only in *Rutilus* does the anterior edge of the exoccipital penetrate forward so as to separate the prootic and epioccipital.

6. *Dilatator fossa*

Ctenopharyngodon (Fig. 10); formed mostly from the sphenotic which extends laterally with a small anterior contribution from the frontal; the frontal border forms a medial roof to the fossa.

Hypophthalmichthys (Fig. 10); formed in almost equal parts from the frontal and sphenotic and sloped antero-laterally as a broad shelf.

The plesiomorph condition of the dilatator fossa in cyprinids is considered to be one in which the fossa is small and formed from nearly equal portions of the frontal, sphenotic and pterotic, and to be roofed or partially roofed by the frontal. This type of fossa morphology is widespread amongst cyprinids and is represented in *Ctenopharyngodon*. An almost identical type of dilatator fossa morphology in characoids is regarded by Vari (1979) as plesiomorphic. In siluroids there is no cranial fossa, the *dilatator operculi* muscle originating from the ventral cranial surface (see Alexander, 1964). Similar ventral muscle origin is to be found in some cyprinids and characoids (see below; Alexander, 1964; Howes, 1978). In most catostomids the dilatator fossa is well developed and involves the sphenotic and the medial part of the frontal. Cobitids (*sensu lato*) possess a small fossa of the type which involves mostly the sphenotic.

It would seem that from the plesiomorphic type of dilatator fossa two avenues of development were open. One was toward extended coverage of the cranial roof, involving mostly the frontal. The second was for the frontal to become invaginated ventro-medially and be pierced by the *dilatator operculi*. The most derived state of the first morphotype in cyprinids is that in *Hypophthalmichthys* where the major contributing elements to the fossa are the frontal and sphenotic, the pterotic being virtually excluded. The sphenotic extends laterally as a broad, ventrally sloping shelf confluent with the frontal. The lateral part of the frontal also slopes and medially bears a ridge which forms the border of the fossa. A similar form of dilatator fossa occurs in *Xenocypris* and *Abramis*, but in these genera the frontal and sphenotic have a more acute ventral slope.

The most derived state of the second morphotype is that where a divided *dilatator operculi* muscle passes through a frontal foramen and a fenestra between the frontal and sphenotic (see below).

These two morphotypes embrace the four enumerated by Howes (1978). Type 1 is described above as the plesiomorph condition and Types 2 and 3 are morphoclinal stages in the encroachment of the cranial surface.

Within the second lineage (Type 4 of Howes, 1978), in which the *dilatator operculi*

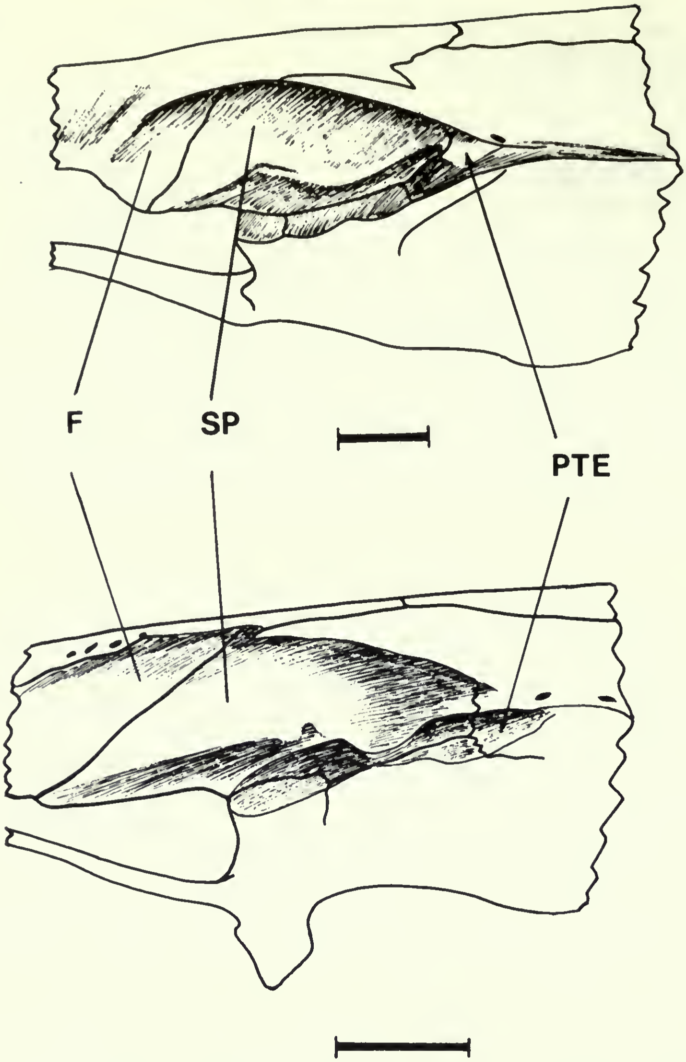


Fig. 10 Dilatator fossae: (upper) *Ctenopharyngodon*; (lower) *Hypophthalmichthys*. Scales = 5 mm. Specimens as previous figure.

originates from the ventral surface of the frontal, a possible transitional sequence can be distinguished. An early stage is hypothesized as being represented by *Squaliobarbus*. Here the frontal is deeply indented anteriorly to the sphenotic and contains a small foramen which enters the orbital cavity. In *Barbus* and *Capoeta* the muscle has 'broken through' the frontal to attach to its ventral surface inside the orbital cavity. A previous statement (Howes, 1978) to the effect that the frontal and sphenotic in *Barbus* contacted each other only along their lateral margins is incorrect. The anterior margin of the sphenotic is bordered by the frontal, albeit in some instances an extremely thin segment (Fig. 11). *Carassius* and *Cyprinus* appear to mark a further stage in development of the foramen for there is in some specimens an almost complete separation between the frontal and sphenotic, the ventro-lateral part of the frontal extending only part way along the sphenotic margin. *Cyprinus* is the more derived taxon in this respect since it has an almost complete frontal-sphenotic foramen (Fig. 11). *Labeo* and *Garra* appear to represent the most derived state, with the *dilatator operculi* being divided, the upper section passing through a frontal foramen, the lower through a foramen between the frontal and a strut-like sphenotic process (Fig. 11). The doubly foraminate forms

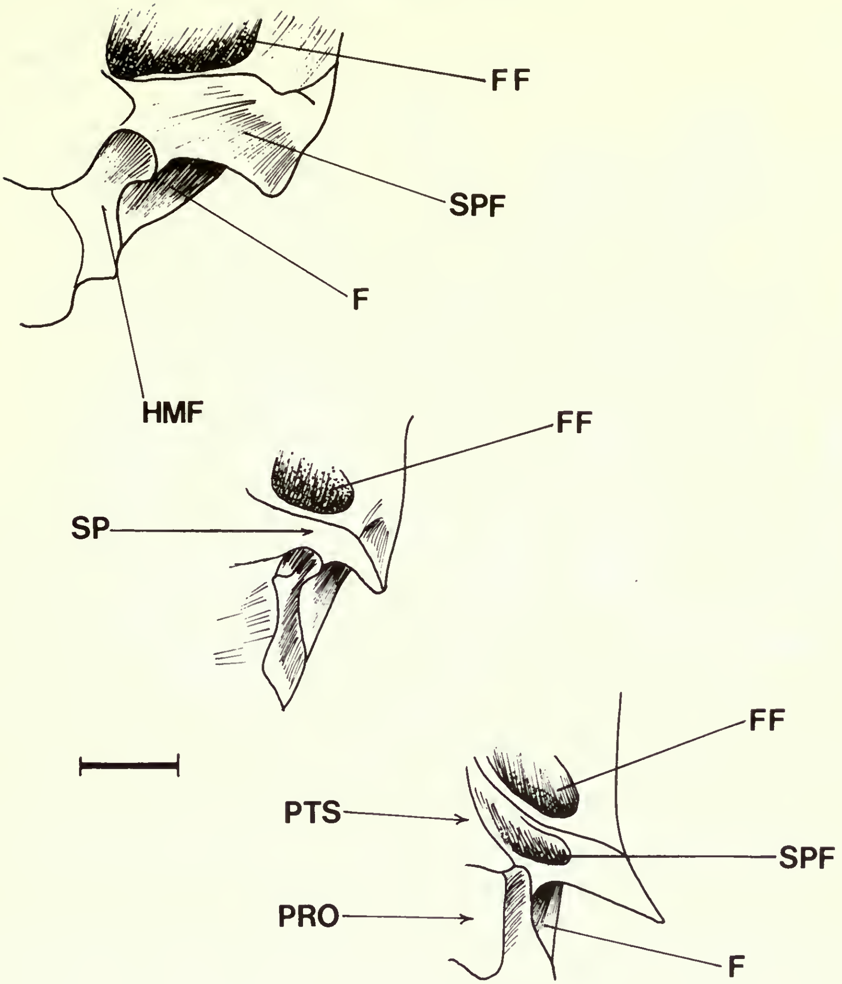


Fig. 11 Dilatator fossae: (upper) *Cyprinus carpio* (uncatalogued); (centre) *Capoeta capoeta* BMNH 1879.11.14 : 19; (lower) *Labeo coubie* BMNH 1907.12.2 : 3744.

of dilatator channel appear to be rewarding characters for the classification of those taxa in which they occur and work in preparation discusses the feature in more detail (Banister & Howes, in preparation).

7. *Frontal*

Ctenopharyngodon (Fig. 12); broad and short, forming 50% of the cranial length (anterior tip of the ethmoid to the posterior border of the parietal), 5–6 pores in the embedded sensory canal, lateral part sloping ventrally at 27° to the transverse plane, a triangular depression occurs above the supraorbital.

Hypophthalmichthys (Fig. 12); broad anteriorly, narrow posteriorly, forming 75% of the cranial length; anterior lateral part sloped ventrally at 45°; sensory canal is an osseus tube on the surface, with 9–10 pores.

In cyprinids, the plesiomorph condition of the frontal is considered to be short and broad (Howes, 1978 : 31). Only in derived members of monophyletic lineages are the frontals elongate, with an increased number of sensory pores. The raised tubular sensory canal, as in *Hypophthalmichthys*, is a feature Tretiakov (1946) used in marking *Tinca* as a primitive cyprinid related to catostomids—which also possess this character. However, in catostomids

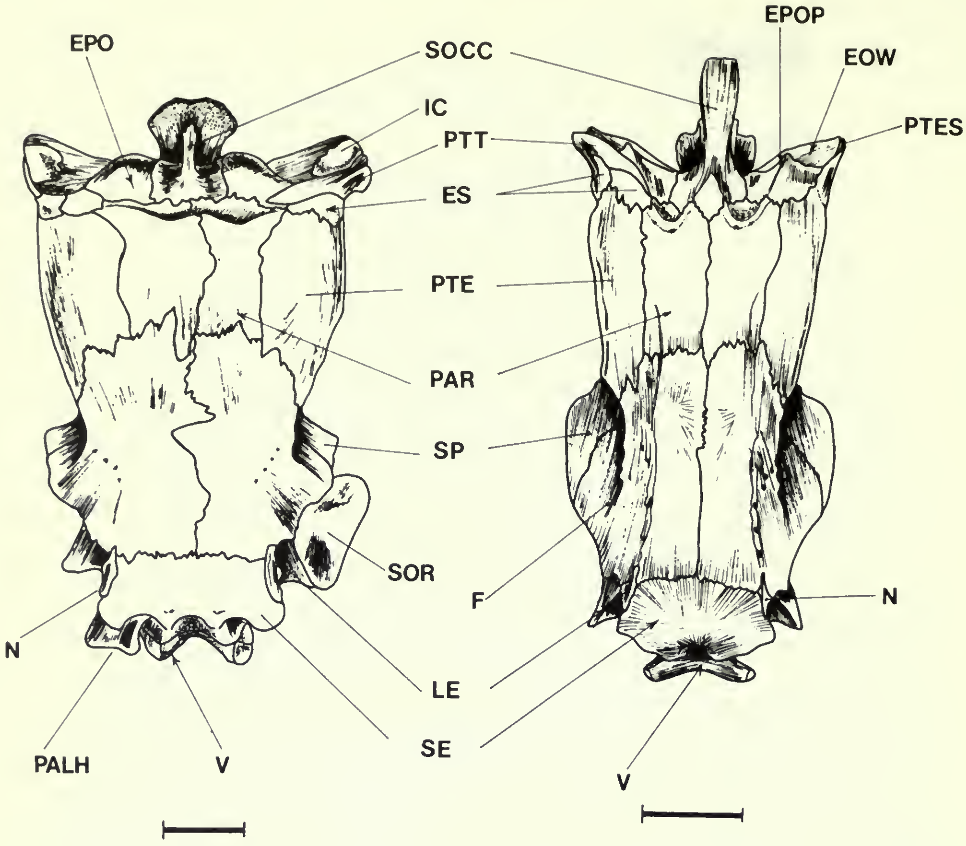


Fig. 12 Dorsocrania: (left) *Ctenopharyngodon*; (right) *Hypophthalmichthys*. Scales = 20 mm. Specimens as previous figures.

the situation is rather different for here the canal is mostly detached from the frontal and runs at the surface of thick subcutaneous tissue covering the cranium (see comments by Sagemahl, 1891 : 508 and Weisel, 1960 : 122). Although raised frontal canals are an uncommon feature in Cyprinidae they occur in abramine genera (see p. 45 for included genera), some cultrines and some chelines (eg. *Oxygaster*). This pattern of ossification has possibly been derived independently in these several groups.

The frontal morphology in *Ctenopharyngodon* is generally of the plesiomorphic type but sloped and laterally depressed, extended border of the bone is a derived state and shared with *Mylopharyngodon*. The markedly sloped frontal in *Hypophthalmichthys* is shared only with *Xenocypris* and *Abramis*.

8. *Parietal*

Ctenopharyngodon (Fig. 12); as broad as the frontal and half its length.

Hypophthalmichthys (Fig. 12); half the greatest width of the frontal and 65% of its length.

Commonly in cyprinids, the parietal is short, being 30%–50% of the frontal length. A parietal fontanelle is usually absent in Cyprinidae but may be found in specimens of *Cyprinus* and various gobioines (see Ramaswami, 1955*a*). This feature, widespread in other otophysans is possibly a plesiomorph character and closure of the fronto-parietal fontanelle is to be regarded as apomorphic for the Cyprinidae (see also Fink & Fink, 1981).

9. *Circumorbital bones*

Ctenopharyngodon (Fig. 13); 1st infraorbital thick and curved outward, 2nd and 3rd

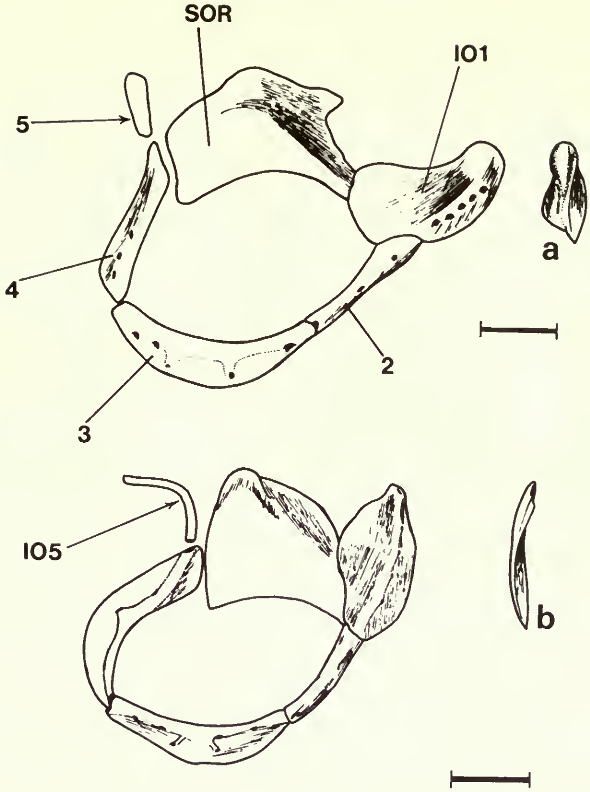


Fig. 13 Circumorbital bones: (upper) *Ctenopharyngodon*; (lower) *Hypophthalmichthys*. a and b are anterior views of the respective 1st infraorbitals. Scales = 10 mm.

infraorbitals elongate, 4th almost perpendicular, 5th long, crossing the sphenotic; supraorbital extensive.

Hypophthalmichthys (Fig. 13); 1st infraorbital thin, vertically aligned; 2nd, 3rd and 4th elongate, 5th, an almost right-angled bone, the vertical portion crossing the frontal, the horizontal part across the sphenotic; supraorbital extensive.

In both genera the supraorbital is extensive and has the effect of extending ventrally the lateral border of the cranial roof so that the ventral edge of the supraorbital comes to lie in the same horizontal plane as that of the parasphenoid. In *Ctenopharyngodon* the supraorbital slopes laterally at the same angle as the frontal, its medial portion is thickened and anteriorly bears a wide groove. The lower anterior border of the bone contacts the posterodorsal edge of the 1st infraorbital. In *Hypophthalmichthys* the supraorbital is directed almost perpendicularly and its anterior part contacts half the dorsal margin of the 1st infraorbital. In small specimens (up to 100 mm SL), only the canal tube of infraorbitals 2–5 is ossified, the upper part of the 4th being fragmented into as many as four portions (Fig. 14).

Comments made previously concerning infraorbitals (Howes, 1978; 1980) suggested that both extreme reduction and expansion of the elements could be seen as derived states. Of these the most often encountered condition in cyprinids is for there to be a reduction of infraorbital ossification, particularly that of the 5th bone, and also this bone's dissociation from the supraorbital.

Gosline (1974) made much of the type of infraorbital-supraorbital sensory canal connection, dividing cyprinids into two groups on the basis of whether or not there was a continuous connection between the two canal systems. Howes (1978) refuted this suggestion by noting that there was always some kind of connection between the canals. What is

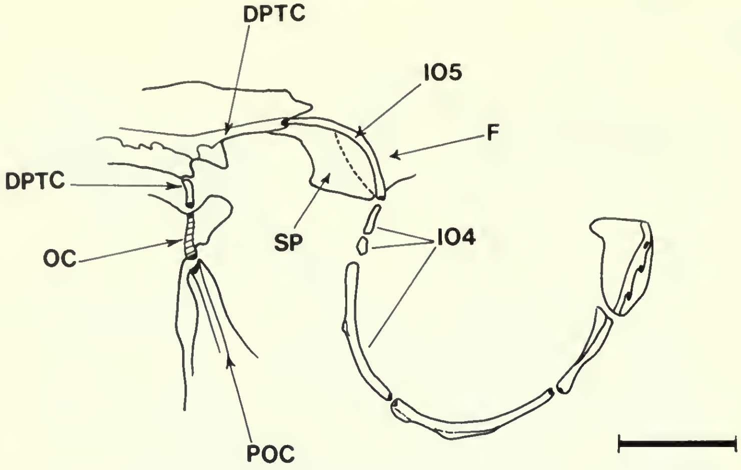


Fig. 14 Circumorbital bones and opercular-pterotic canal system of *Hypophthalmichthys molitrix*. Drawn from an alizarin specimen 65 mm SL. Scale = 3 mm.

possibly of more significance is the form of the 5th infraorbital and its association with the dermosphenotic. Contrary to a previous statement (Howes, 1978) the dermosphenotic is present in many cyprinids (the element labelled as a dermosphenotic in *Oreoleuciscus* [Howes, 1978, fig. 22] appears to be the fragmented 5th infraorbital, and that in *'Chelaethiops'* [Fig. 23] part of the dermopterotic). The distribution of the dermosphenotic amongst cyprinids and the morphology of associated canal systems is discussed in a separate paper (Banister & Howes, in preparation).

The thickened 1st infraorbital of *Ctenopharyngodon* is an autapomorphic feature, although there is a tendency towards thickening of that bone in *Mylopharyngodon*. Both genera, however, share the derived, massive ridged supraorbital. Similarly, the enlarged supraorbital of *Hypophthalmichthys* is shared with *Xenocypris*. But, again the infraorbital pattern of *Hypophthalmichthys* is autapomorphic.

10. *Supraoccipital*

Ctenopharyngodon (Fig. 12); short with posterior lamellate process.

Hypophthalmichthys (Fig. 12); long with dorsally thickened crest.

The supraoccipital of *Ctenopharyngodon* is the type most commonly present in Cyprinidae *viz* an almost square bone with a low crest. The broad, thick supraoccipital crest of *Hypophthalmichthys* is not encountered elsewhere in the cyprinids. Another autapomorphic feature occurring in this genus is that the anterior portion of the supraoccipital is on a raised platform, the sides of which are contributed by the parietals.

11. *Exoccipital*

Ctenopharyngodon (Fig. 15); contains a fossa posterior to the subtemporal fossa; the postero-ventral border of the bone is horizontal.

Hypophthalmichthys (Fig. 15); without supplementary fossa; postero-ventral border sloping laterally and caudally.

An earlier statement (Howes, 1978 : 38) claimed that in cyprinids the exoccipital showed little variability. This is not the case in the two genera now under discussion.

In *Ctenopharyngodon* the posterior border of the exoccipital lateral wall is horizontal—a condition considered plesiomorphic on account of its widespread distribution. The dorsal part of the bone, immediately posterior to the subtemporal fossa, bears a shallow depression (also contributed to by the intercalar—see below). From this supplementary fossa there arises a posterior section of the *levator posterior* muscle.

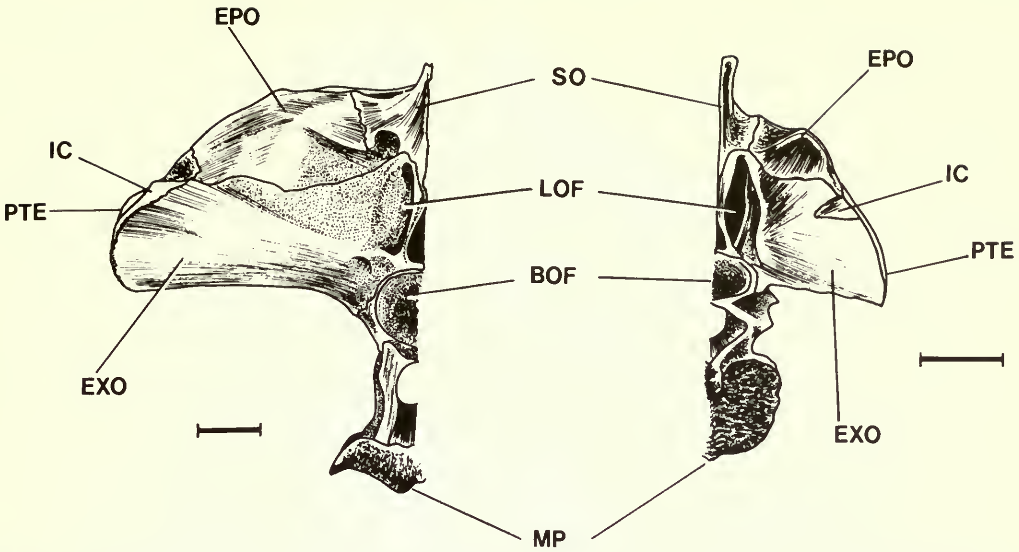


Fig. 15 Posterior cranial region: (left) *Ctenopharyngodon*; (right) *Hypophthalmichthys*. Scales = 10 mm. Specimens as previous figures.

In *Hypophthalmichthys* the posterior exoccipital wall slopes ventrally at an angle of 45° to the horizontal, its ventral border is also directed laterally at a similar angle with the result that the entire wall forms a triangular wing. The postero-lateral flaring of the exoccipital wall is so great that its distal edge contacts the distal tip of the pterotic spine—a feature otherwise present only in *Xenocypris*. In all other cyprinids examined the pterotic spine is separated from the exoccipital margin by a substantial part of the pterotic floor or by the intercalar. The dorsal surface posterior to the subtemporal fossa is flat, the *levator posterior* taking its origin entirely from the subtemporal fossa.

A *levator posterior* with a section originating from a supplementary subtemporal fossa as in *Ctenopharyngodon* is known elsewhere only in *Mylopharyngodon* and *Squaliobarbus* and is considered synapomorphic.

The *lateral occipital fenestra* in *Ctenopharyngodon* is narrow and when viewed posteriorly is obscured by the exoccipital medial border; a feature which otherwise occurs only in *Mylopharyngodon*. In contrast, there is an extensive fenestra in *Hypophthalmichthys*. In the Cyprinidae there is quite some variation in the size and shape of the fenestra although usually it is small and ovate. Rarely does it have the proportions of that in *Hypophthalmichthys*, which are approached only by *Xenocypris* and *Abramis*. To my knowledge, the fenestra is never reduced to the extent of *Ctenopharyngodon* and *Mylopharyngodon*. Both these conditions may be recognized as derived states.

12. *Epioccipital*

Ctenopharyngodon (Fig. 15); bullate with a slight posterior ridge; posttemporal fossa exists as a mere depression between the epioccipital and the pterotic.

Hypophthalmichthys (Fig. 15); triangular with a prominent posterior lip below which is a depression of the epioccipital wall; posttemporal fossa well-developed, extending someway anteriorly between the epioccipital and pterotic.

The epioccipital in *Ctenopharyngodon* is greatly developed and contributes the major part to the formation of the subtemporal fossa. As in all cyprinids the epioccipital roof provides the major site of origin for the *levator posterior* muscles (see Eastman, 1971). The bone in *Hypophthalmichthys* is virtually pyramidal and posteriorly has a broadly pointed lip. This lip or shelf serves for the attachment of hypaxial musculature and although variously developed throughout cyprinids in none is it more so than in this taxon.

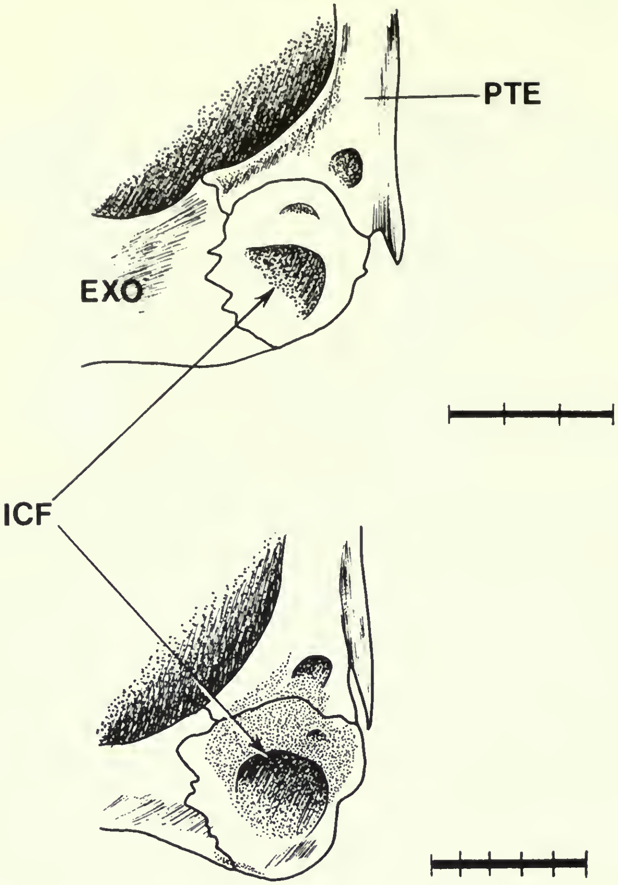


Fig. 16 Intercalar: (upper) *Squaliobarbus curriculus* BMNH 1888.5.15 : 29; (lower) *Mylopharyngodon piceus* BMNH 1895.5.31 : 40. Scales in mm divisions.

13. *Intercalar*

Ctenopharyngodon (Fig. 16); extensive and forming the posterior corner of the cranium between the basioccipital and pterotic. Its ventral surface contributes to the supplementary subtemporal fossa (see above) and provides the site of origin for the posterior section of the *levator posterior* muscle.

Hypophthalmichthys (Fig. 16); smaller than the former taxon, when viewed posteriorly is seen as a triangular wedge intruding into the lateral border of the exoccipital (Fig. 15). Its ventral surface is broad and lies between the exoccipital and medial edge of the pterotic spine (Fig. 9). The intercalar morphology of *Hypophthalmichthys* is autapomorphic.

In cyprinids the intercalar is transitory, as for example in the aspinine group (see Howes, 1978) where it is well-developed in most members, but absent in the more derived taxa. Rarely is the intercalar developed to the extent that it is in *Ctenopharyngodon* and occurs similarly only in *Mylopharyngodon* and *Squaliobarbus* (Fig. 16) where it also provides the site of origin for part of the *levator posterior* muscle.

In *Capoeta* the intercalar also contributes to the area of origin of the *levator externus* (Fig. 17). However, in this genus the intercalar forms the lateral border to the exoccipital. The posterior wall of the exoccipital is strongly concave and provides the site of origin for the remainder of the posterior segment of the *levator* muscle. The exoccipital wall is strongly concave and its lateral margin is separated by a wide gap from the pterotic spine. In *Cyprinus* and *Carassius* the posterior wall of the exoccipital is virtually identical to that of *Capoeta.*

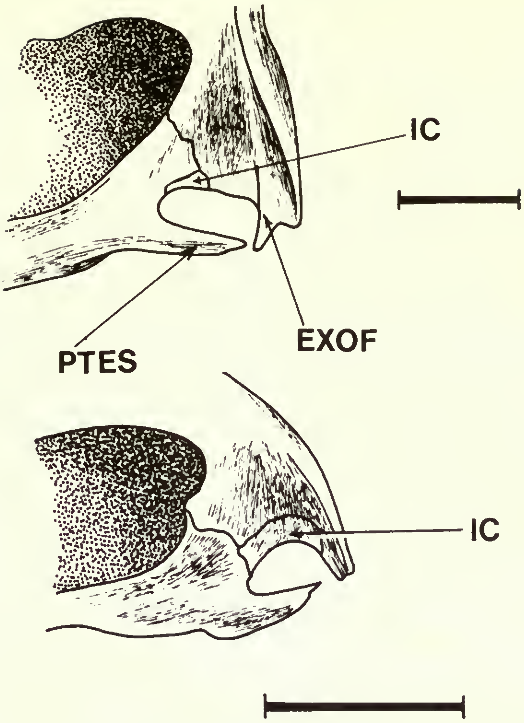


Fig. 17 Postero-ventral region of the cranium: (upper) *Cyprinus carpio* (uncatalogued); (lower) *Capoeta capoeta* BMNH 1879.11.14 : 19. Scales = 5 mm.

However, in these two genera, the intercalar is minute (or may even be absent) and is confined to the lateral edge of the pterotic; it plays no part in providing an area of attachment for the *levator posterior* muscle.

14. *Basioccipital*

Ctenopharyngodon (Fig. 19a); ventral keel shallow, concave anteriorly; masticatory plate large and ovate with a shallow ventral depression; pharyngeal pad thick, lozenge shaped with a longitudinally ridged surface; pharyngeal process broad and thick, its distal end rounded and upwardly curved; basioccipital facet circular.

Hypophthalmichthys (Figs 18a & 19e); ventral keel deep with markedly concave anterior border; masticatory plate cardiform, cancellous with a thick anteriorly directed point; pharyngeal pad thin, keratinized, its surface bearing a median ridge; pharyngeal process elongate, cylindrical and ventrally directed; basioccipital facet ovate.

Although there is quite some variation in the morphology of the basioccipital keel and its associated masticatory plate, that of *Hypophthalmichthys* is outstanding in its length and shape. Only in *Xenocypris* and *Distoechodon* is there a similar degree of development of the basioccipital keel (see illustrations in Tomodo, 1979 : 96). The ventral prolongation of the basioccipital in *Hypophthalmichthys* is associated with the epibranchial organs and serves for the attachment of the epibranchial duct and a medial ligament that stems from the cartilaginous bloc running along the midline. Genera which most closely approach *Hypophthalmichthys* and *Xenocypris* (including here *Distoechodon*) are *Rutilus* and *Chondrostoma* (Figs 18d & c). In these genera and *Abramis*, the ventral border of the basioccipital just anterior to the aortic foramen is formed into a deep channel. The most derived condition is in *Abramis* where a rounded notch indents the ventral border of the bone. The basioccipital channel is confluent with a similar feature of the parasphenoid (see p. 12) and is filled with cartilage.

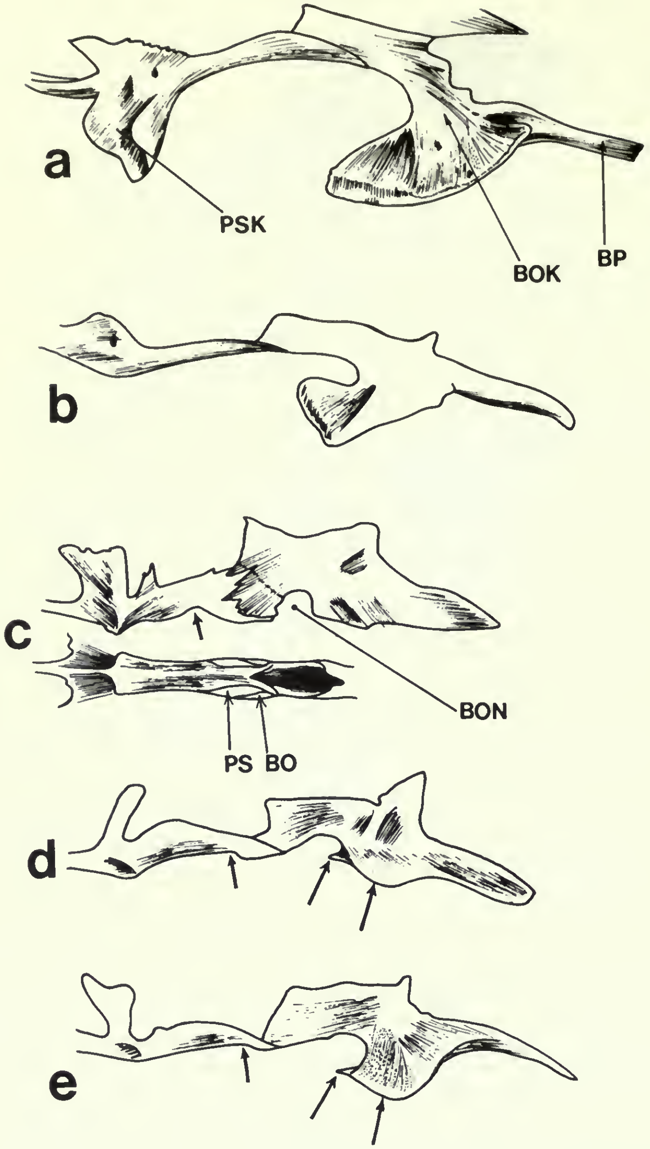


Fig. 18 Basicrania in lateral view: a. *Hypophthalmichthys molitrix*; b. *Xenocypris argenteus*; c. *Abramis brama*; d. *Rutilus rutilus*; e. *Chondrostoma nasus*. *Abramis* (c) is also shown in ventral view. The solid arrows indicate considered apomorphic features of the parasphenoid-basioccipital. Composites, all drawn to same scale.

The shape and size of the basioccipital masticatory plate is variable in the Cyprinidae. Being part of the pharyngeal feeding mechanism it would be expected that a particular pharyngeal dentition would be associated with a specific plate morphology. By and large this appears to be the case; the most common type of plate is a small triangular one with a compressed triangularly shaped posterior process. This morphology is associated with omnivorous or piscivorous dental types (simple, often single-rowed, recurved teeth). The pharyngeal plate of *Ctenopharyngodon* greatly resembles that of *Squaliobarbus* and *Rutilus* (Figs 19a, c & d), both regarded as being plesiomorphic. However, the posterior pharyngeal process is of a unique type whereas that in *Rutilus* and *Squaliobarbus* is of the plesiomorphic form. *Mylopharyngodon* exhibits a derived, bowl-shaped plate—associated with molariform

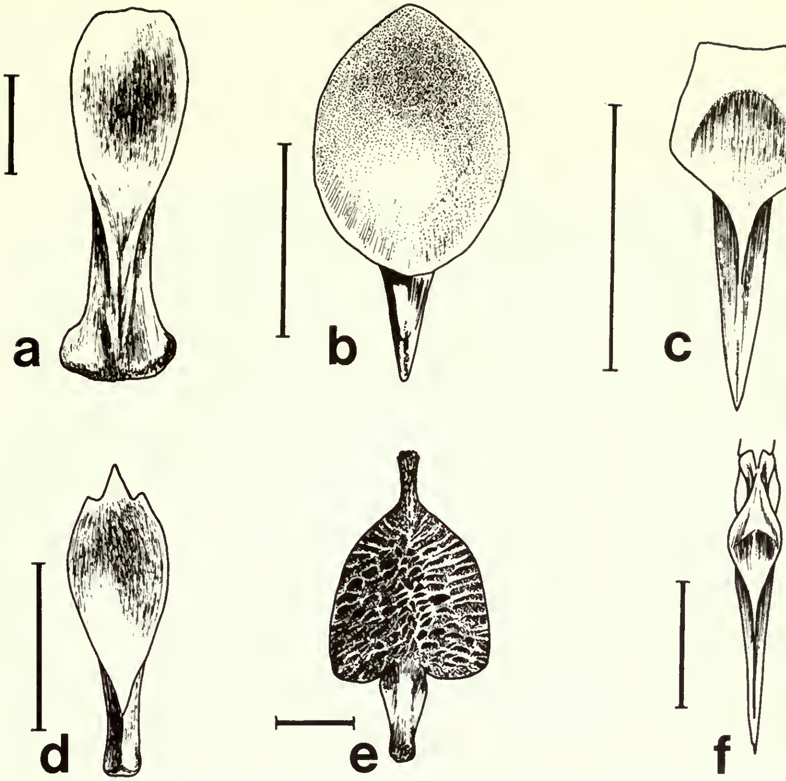


Fig. 19 Basioccipital masticatory plates: a. *Ctenopharyngodon idellus* BMNH 1888.5.15 : 25; b. *Mylopharyngodon piceus* BMNH 1895.5.31 : 40; c. *Squaliobarbus curriculus* BMNH 1888.5.15 : 29; d. *Rutilus rutilus* uncatalogued skeleton; e. *Hypophthalmichthys molitrix* BMNH 1895.5.31 : 22; f. *Abramis brama* uncatalogued skeleton. Scales = 10 mm.

dentition—but one obviously little modified from the plesiomorphic pattern and seemingly achieved by lateral and posterior expansion (Fig. 19b). A similarly developed plate type is found in *Labeo* species but here, the pharyngeal process is differently modified, forming a roof over the aortic channel (Reid, 1978, unpublished thesis). Another derived state occurs in *Abramis* where the pharyngeal plate has virtually disappeared (Fig. 19f). Extreme reduction is also found in *Semiplotus,* but a characteristic surface and aortic channel morphology is apomorphic for this taxon.

It is thus concluded that particular details in the morphology of the basioccipital plate and posterior process can be useful indicators of relationship.

15. *Posttemporal*

Ctenopharyngodon (Fig. 12); broad, straight with long dorsal arm, basal part of the bone applied to the pterotic and intercalar, its upper part bridges the shallow posttemporal fossa to lie against the epioccipital. The anterior margin of the dorsal extension is bordered by a broad extrascapula.

Hypophthalmichthys (Fig. 12); elongate with a broad paddle-shaped basal portion, its upper half narrow and pointed distally. The anterior border of the bone curves round the posterior margin of the extrascapula. The *extrascapula* is elongate with an irregular anterior margin.

The *Ctenopharyngodon* type of posttemporal and extrascapula is widespread throughout the cyprinids and is regarded as plesiomorphic. The curved, spine-like posttemporal and narrow extrascapula of *Hypophthalmichthys* is otherwise present only in *Xenocypris.*

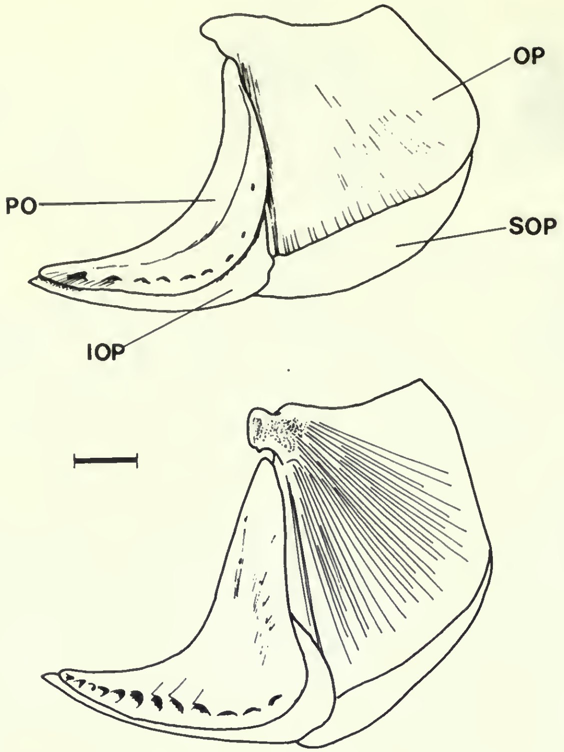


Fig. 20 Opercular bones: (upper) *Ctenopharyngodon idellus* BMNH 1861.1.17 : 6; (lower) *Hypophthalmichthys molitrix* BMNH 1895.5.31 : 22. Scale = 10 mm.

16. *Opercular bones*

Ctenopharyngodon (Fig. 20); preoperculum with a shallow horizontal limb containing 6 pores of the sensory canal system; operculum large, almost square.

Hypophthalmichthys (Fig. 20); preoperculum with deep horizontal limb containing 15 sensory pores; operculum large, deeper than long, its outer surface strongly ridged.

In both genera the basal part of the antero-dorsal opercular process (to which is attached the tendon of the *dilatator operculi* muscle) contains a tubular canal connecting the preopercular canal with the pterotic canal. The connection between the operculum and the pterotic in *Hypophthalmichthys* is effected through an ossified canal lying vertically above the opercular process. This small canal-carrying bone appears to be part of the dermopterotic.

There appears to be some variability in the morphology of the opercular sensory canal. Gosline (1974) noted that the preopercular canal ends 'blindly' or passes across the opercular face. However, where there is a connection between the preopercular and pterotic canals, it can be *via* a dermal opercular canal or 'suprapreopercula', an opercular tube or an epidermal connection. These varying conditions and their taxonomic significance are discussed in a separate paper (Banister & Howes, in preparation).

The opercular series, and particularly the size of the operculum are somewhat variable throughout the Cyprinidae but certain types of opercula can be associated with particular monophyletic groups. Examples are the bariliines where the opercular bones are almost always deep and narrow; the neobolines (*Chelaethiops, Neobolus*) where the opercula have an attenuated posterior margin; the chelines and aspinines where the opercula possess a long dorsal border. Caution must be exercised, however, in using opercula bone morphology as a phyletic character. Large opercular and expanded preopercular bones are to be found in such widely different trophic specialists as *Luciobrama, Barbus, Ctenopharyngodon* and

Hypophthalmichthys. In these taxa the similarity of opercular bone shapes appear to be the result of different functional demands which are at present not understood.

17. *Suspensorium*

Overall, there is a great similarity in the suspensorial elements of *Ctenopharyngodon* and *Hypophthalmichthys.*

The *palatine* is broad anteriorly in both genera. However, in *Ctenopharyngodon* articulation of the palatine head is with the lateral supraethmoid notch (see p. 5; Fig. 1). The more usual condition is for the palatine head to be at a lower level, almost in the plane of the preethmoid and to be attached by a ligament to either the anterior rim, the ventral surface of the supraethmoid, or to the upper part of the mesethmoid. Only in *Mylopharyngodon* and *Squaliobarbus* is the palatine head elevated as in *Ctenopharyngodon* and closely articulated with a lateral supraethmoid notch. The posterior part of the palatine in *Ctenopharyngodon* is rounded and articulates in a deep entopterygoid facet. The posterior region of the palatine in *Hypophthalmichthys* is laterally compressed and articulates with a shallow, narrow entopterygoid facet. Both types of posterior palatine articulation are encountered widely in cyprinids and it is not possible at present to say which is the more derived.

In both genera the *hyomandibula* is produced laterally and its articulatory dorsal border is steeply angled antero-ventrally. However, in *Ctenopharyngodon* there is a lateral shelf on the upper face of the hyomandibula and the ventral limb of the bone is short and broad, whereas in *Hypophthalmichthys* it is elongate. In both genera the *entopterygoid* and *metapterygoid* are depressed medially with the metapterygoid having a strongly concave dorsal border and a well-defined lateral ridge; the *quadrate* bears a wide ventro-lateral shelf, but in *Ctenopharyngodon* it is a larger bone than in *Hypophthalmichthys.*

There are differences in the form of the *symplectic* which is elongate in *Hypophthalmichthys* but short and deep in *Ctenopharyngodon.* This latter type appears to represent the more derived condition (see Howes, 1980), the elongate symplectic being common in Cyprinidae.

In general, there is uniformity of the suspensorial elements in the Cyprinidae; the variability is one of degree, usually involving elongations, deepening or medial depression of the bones.

18. *Jaws*

Ctenopharyngodon (Figs 21d, e, f); *maxilla* deep with a triangular midlateral ascending process; the anterior medial process is directed almost horizontally to contact its partner *via* a ligament; maxillary distal portion is broad, medially curved and produced into a ventral flange which contacts the distal part of the premaxilla. Approximately mid-way along the maxilla is a foramen sited below a lateral ridge (which serves as the attachment for the palatine ligament). The *premaxilla* is deep with only a short anterior ascending process its ventral edge is chisel-like. The *dentary* has a short, dorsally rounded coronoid process; the *anguloarticular,* a convex dorsal border.

Hypophthalmichthys (Figs 21a, b, c); *maxilla* shallow with a high, square midlateral ascending process; the anterior medial process is compressed and directed ventrad toward the midline; maxillary posterior portion is laterally compressed and ventrally extended to articulate with the premaxilla. The *premaxilla* is exceedingly shallow and thin with a short, broad, anterior ascending process and although its ventral edge is sharp, it is not bevelled as in *Ctenopharyngodon.* The *dentary* is shallow at the symphysis but deepens posteriorly and has a high, backwardly sloped coronoid process. The *anguloarticular* is short and deep with a long, steep dorsal border (60° slope to the horizontal).

The plesiomorphic cyprinid maxilla appears to be of the *Ctenopharyngodon* type, *viz* deep, with a large mid-lateral, or posteriorly placed ascending process with convex anterior, and concave posterior borders. Apomorphic derivatives involve the formation of a concave anterior border to the mid-lateral process as in *Hypophthalmichthys*, or complete reduction

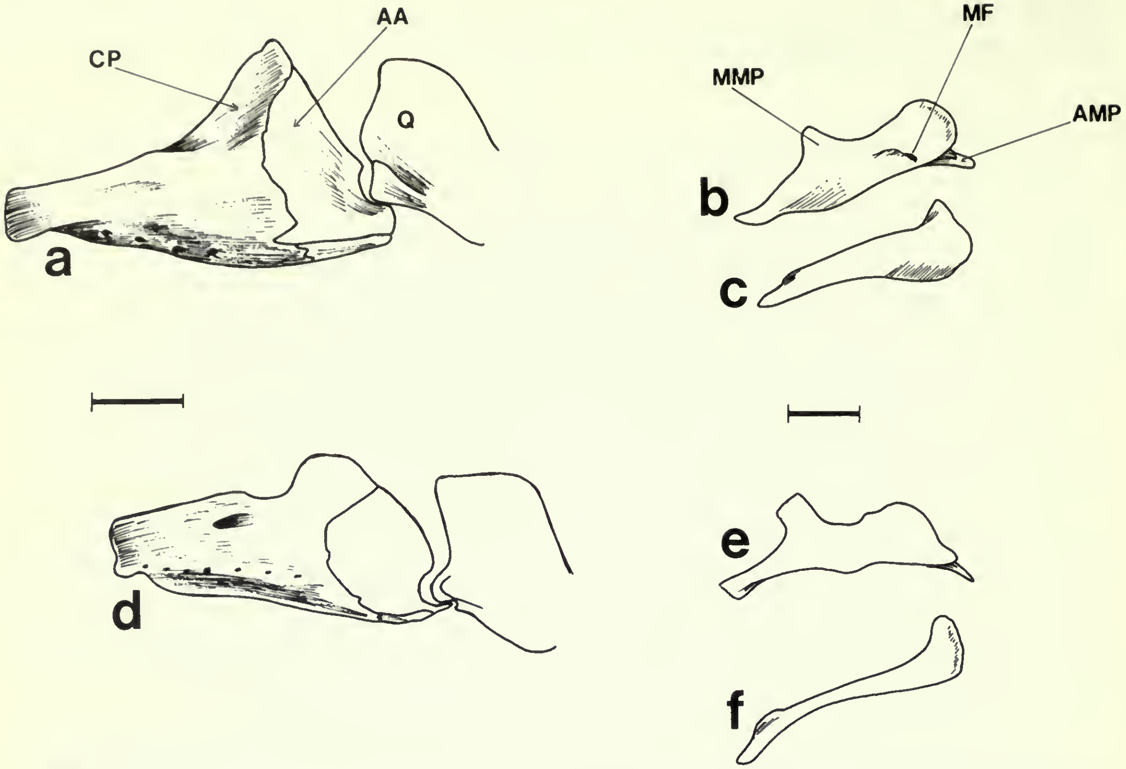


Fig. 21 Jaw bones in lateral view: *Hypophthalmichthys*, a. left dentary, b. right maxilla and c. right premaxilla; *Ctenopharyngodon*, d. left dentary, e. right maxilla and f. right premaxilla. Scales = 10 mm.

of the process as in some bariliines (see Howes, 1980). Another apomorphic feature of the maxilla appears to be the presence of an anterior foramen. This foramen provides the channel for a branch of the facial nerve which usually innervates an associated barbel. Although such a foramen is present in *Ctenopharyngodon*, there is no associated barbel and it will be argued later that this is due to secondary loss of the barbel (see p. 39). For the most part, however, it is true to say that those cyprinids with a maxillary foramen also have a rostral barbel. One cyprinid group which lack the maxillary foramen but have barbels are some bariliines (see Howes, 1980). However, in these taxa the barbel is not associated with the maxillary bone. The phylogenetic significance of these various conditions is discussed elsewhere (Banister & Howes, in preparation), but here it can be stated that the presence of a maxillary foramen is an apomorphic feature in one group of Cyprinidae (see also Banister & Bunni, 1980 : 157).

An L-shaped premaxilla without any dorsal or lateral protruberances is thought to represent the plesiomorph condition.

Although superficially alike, the lower jaws of *Ctenopharyngodon* and *Hypophthalmichthys* differ in the form of the coronoid process and anguloarticular. In the Cyprinidae the most common type of lower jaw morphology is one where the coronoid process occupies a central position and is formed entirely from the dentary. In these cases the anguloarticular has an almost horizontal dorsal border (eg. *Barbus, Leuciscus, Aspius, Culter*; see fig. 36 in Howes, 1978). Contribution of the anguloarticular to the coronoid may be considered derived and associated with orientation of the jaw and a shift in mandibular muscle insertions. A lower jaw element which may be worthy of more critical attention in cyprinids is the *coronomeckelian* bone. It commonly occurs as a deep, short bone with a well-developed shelf along its medial face to which attaches the tendon of part of the *adductor*

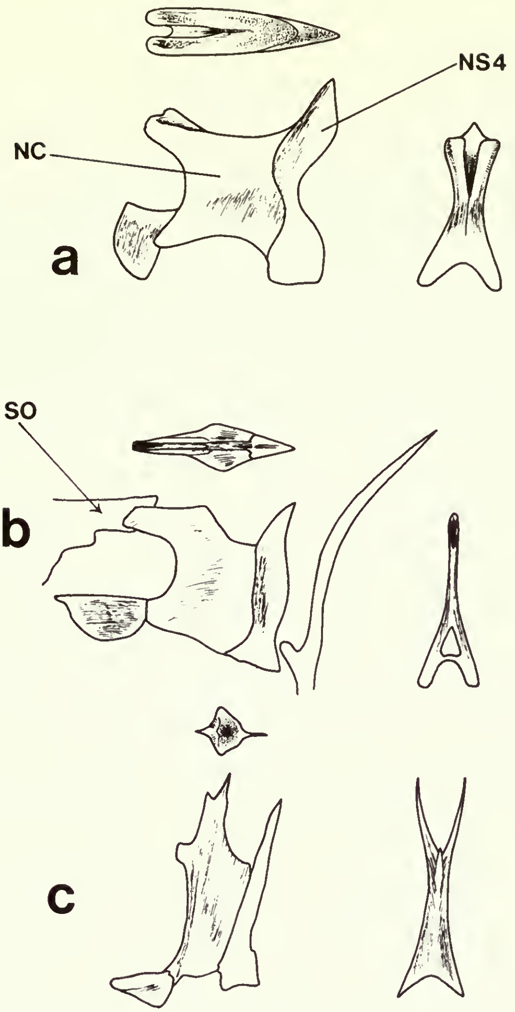


Fig. 22 Anterior dorsal vertebral elements shown in lateral, dorsal and anterior views of: a. *Ctenopharyngodon*; b. *Hypophthalmichthys*; c. *Abramis brama*. Semi-diagrammatic, compiled from several specimens; all drawn to same scale.

mandibulae complex. There is some variation in the shape of this bone and certainly in one group of 'leuciscines' its spear-shaped appearance seems to offer an apomorphic character of phyletic value (Howes, in preparation). The morphology of the lower jaw is possibly the most variable anatomical unit in Cyprinidae, relative growth of its various parts probably being a major contributing factor to this variability.

19. *Vertebral column*

Ctenopharyngodon (Fig. 22a); 1st vertebra compressed and with laterally directed processes, 2nd with an elongate lateral process, 4th with anteriorly sloping pleural rib and backwardly sloping neural spine. Weberian complex: tripus broad, sickle-shaped; ossa suspensoria making extensive medial contact and forming a posteriorly curved transverse septum. Total number of vertebrae 43 (4 + 22 + 16 + 1).

Hypophthalmichthys (Fig. 22b); 1st vertebra with caudally directed lateral processes, 2nd with short, triangular, caudally directed processes, 4th with anteriorly sloping pleural rib and upright neural spine. Weberian complex: tripus elongate with mesially curved tip, ossa suspensoria extensive forming an antero-ventrally sloping transverse septum, neural complex bifurcated and articulating with supraoccipital. Total number of vertebrae 39–40 (4 + 18–19 + 16 + 1).

The most striking differences in the morphology of the vertebral column in *Ctenopharyngodon* and *Hypophthalmichthys* occur in the anterior vertebrae forming the Weberian complex. The neural complex of *Ctenopharyngodon* is antero-dorsally expanded and curved forward so that its anterior tip is above the 1st vertebra (Fig. 22a); there is no contact with the supraoccipital. In *Hypophthalmichthys* the neural plate is deep and lamellate with a concave anterior border. The antero-dorsal prong is bifurcated and the supraoccipital process contained within the fork (Fig. 22b). The dorsal margin of the neural plate is deeply grooved for the midline ligament, as it is in the aspinines (see Howes, 1978 : 19).

In the Cyprinidae contact between the supraoccipital crest and the neural complex is uncommon. It occurs in *Labeo, Catla, Osteobrama* and *Semiplotus,* but in these taxa there is no deeply grooved dorsal margin to the neural complex, and the anterior bifurcation is either shallow or lacking. Only in *Xenocypris* does the neural complex have nearly the same morphology as in *Hypophthalmichthys.* However, a well-developed lamellate neural plate is commonly encountered in the Cyprinidae and may be a plesiomorphic character. In *Abramis, Rutilus* and some species of *Chondrostoma* the neural complex has no antero-dorsal extension but is perpendicular or anteriorly inclined and deeply forked; a condition unique in cyprinids (Fig. 22c). In some catostomids (*Carpoides*) there is contact between the supraoccipital and neural complex. Here the condition is similar to that in *Labeo* where the neural plate is lamellate and without a dorsal groove or anterior bifurcation.

It seems likely that in the latter cases expansion of the neural complex (? fused 3rd and 4th supraneurals) and its contact with the supraoccipital is associated with a deepened body and the forceful forward probing movements of the head when feeding. Reinforcement of the anterior part of the vertebral column and rigidity of the posterior cranium is provided by this arrangement. In *Hypophthalmichthys* which is essentially a mid-water or surface feeder, this feature must serve a different purpose and may be associated with some elevation of the cranium during feeding.

The common (plesiomorph) condition of the first four (Weberian) vertebrae in Cyprinidae is as in *Ctenopharyngodon* (the typical condition is seen in *Opsaridium microcephalus,* Howes, 1980, fig. 39D). Similar development of the transverse processes, tripus and ossa suspensoria similar to those of *Hypophthalmichthys* is encountered elsewhere in members of the 'Leuciscinae' (ie *Leuciscus, Abramis*) and the aspinine group. However, elongation of these elements is also found in some barbines, chelines and neobolines (eg. *Chelaethiops*) and its usefulness as an indicator of phyletic relationship is doubtful.

20. *Gill-arches*

Ctenopharyngodon has no particular modifications of the gill arches, which are similar to those of other cyprinids. The gill-rakers are short and spiny, biserially arranged and almost horizontally placed on the arch so that they intermesh with those on the neighbouring arch to form a filter.

Hypophthalmichthys displays marked modification of the gill arches and possesses a complex epibranchial organ (Figs 24–26).

The gill structures of *Hypophthalmichthys* have been described in varying detail by a number of authors. Boulenger (1901) first described the epibranchial organ; Fang (1928) gave a detailed description of the gill arches and epibranchial organ, and speculated on their function. Zambriborshch (1955; 1957) described and figured the gross morphology of the branchial apparatus and histology of the gill-rakers, including comments on function. Verigin (1957) described and figured the epibranchial organ, gill-rakers, upper pharyngeal pad and roof of the pharynx. He also studied the ontogeny of the branchial apparatus. Wilamovski (1972) made a description of the epibranchial organ and gill-rakers, comparing them with the branchial system of *Cyprinus.* Taken *in toto* these descriptions give an

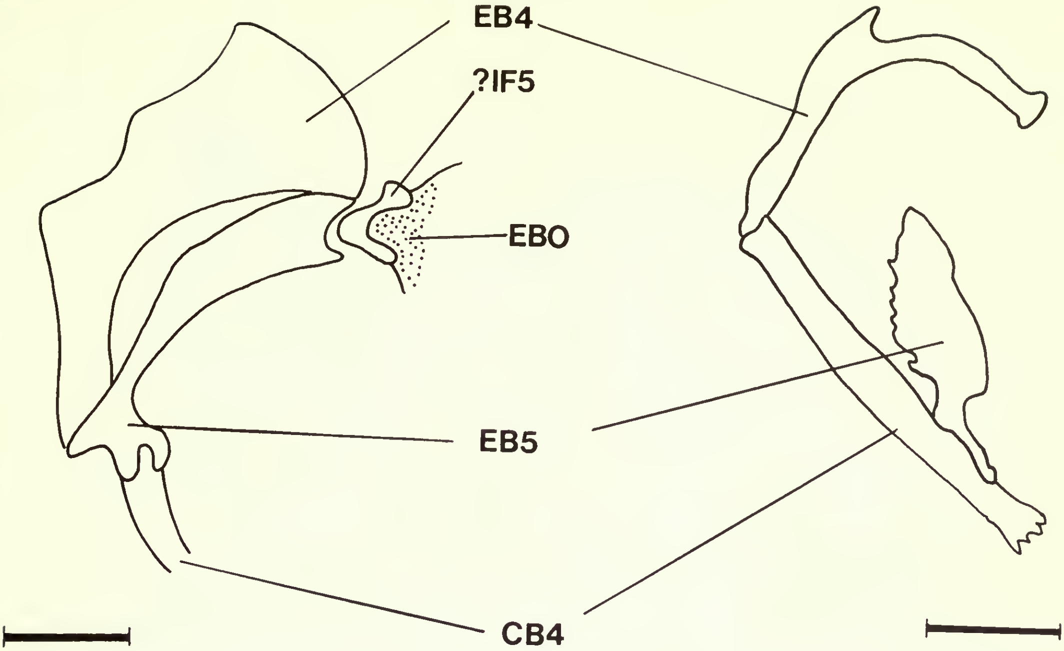


Fig. 23 Posterior gill-arch elements: (left) *Hypophthalmichthys molitrix*, from dissected specimen BMNH 1895.5.31 : 22; (right) *Xenocypris argenteus* from alizarin specimen BMNH 1889.6.8 : 19. Left scale = 5 mm, right = 2 mm.

adequate account of the organ's morphology, and it is necessary here only to emphasize certain of its apomorph characters.

The *ceratobranchials* are elongate, bearing numerous biserially arranged slender gill-rakers. The two rows of rakers are set at a diverging angle to one another thus producing an 'interbranchial space' (Fang, 1928). There are approximately 13–14 rakers per 1 mm of ceratobranchial. Fang (1928) recognized two types of gill-rakers, broad and narrow, the broad type occurring between each 4th and 5th narrow type. The gill-rakers are connected by a reticulate mucuous membrane (sifting membrane of Fang, 1928) which forms a network or filter, whose pores are about 20 μ in diameter. The gill-rakers continue onto the epibranchials.

The 1st and 4th *epibranchials* are expanded dorsally into axe-shaped elements. The 1st forms the anterodorsal wall, and the 4th the posteromedial wall of the epibranchial organ (the branchial arches are so orientated that the 4th epibranchial comes to lie in a medial (longitudinal) plane rather than a posterior (transverse) one). Although not entirely ossified, a 5th epibranchial is present as a well-developed, broad, lamellate element, and has a complex articulation with the 4th ceratobranchial (Fig. 23).

There are two large well-ossified *infrapharyngobranchials* recognized as IF2 and IF3; IF4 is represented by an extensive cartilaginous bloc bordering the posterior rim of IF3 and contacting epibranchials 3 and 4 (Fig. 24). In front of IF2 there is another large cartilaginous cap onto which articulates epibranchial 1. This no doubt is IF1. In adult specimens the 5th epibranchial is joined to the capsule of the epibranchial organ *via* an interposed cartilage which may represent the 5th infrapharyngobranchial.

The *epibranchial organ* is formed by four curled cartilaginous channels or ducts, which are prolongations of the four epibranchials (Fig. 26). Each duct is lined with two rows of biserially arranged gill-rakers, the posterior row of one arch intermeshing with the anterior row of the adjacent arch and in this way running into each duct (Fig. 24). The outer row of the 1st arch enters a small chamber of the first duct and becomes reduced in size and number. The first duct houses the gill-raker rows of the 1st and 2nd epibranchials, the 2nd those of the

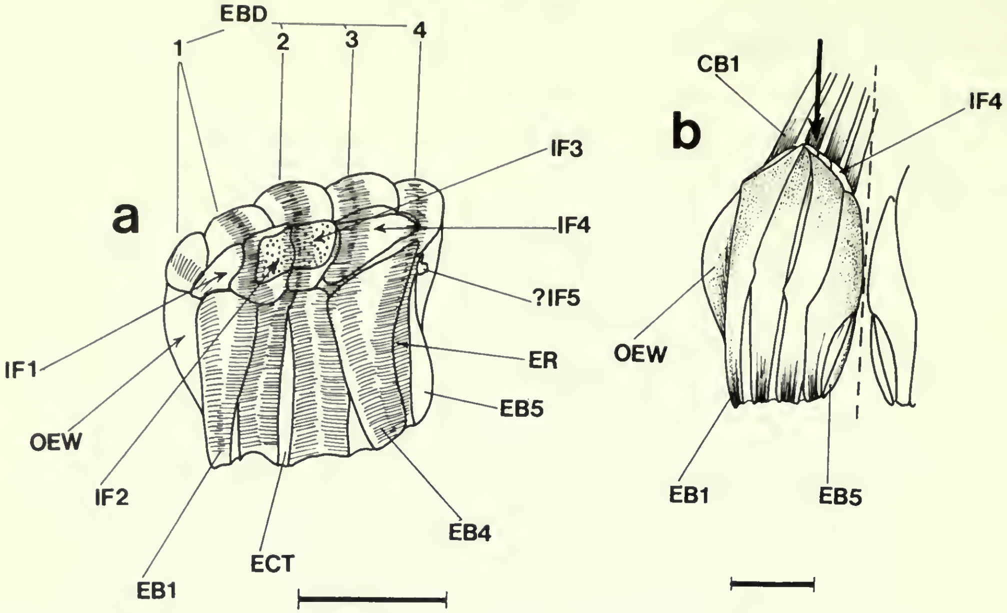


Fig. 24 *Hypophthalmichthys* epibranchial organ: a. anterior view of left organ, ossified areas of the infrapharyngobranchials are stippled; b. dorsal view of left organ to show orientation, dashed line represents the ventral midline of the head, and solid arrow indicates the direction of view depicted in a. Scales = 10 mm.

2nd and 3rd epibranchials, the 3rd those of the 3rd and 4th, and the 4th duct those of the 4th and 5th epibranchials. Zambriborshch (1957) referred to the organ ducts as supra- and infrapharyngobranchials. However, the infrapharyngobranchials are here identified as elements distinct from the cartilaginous ducts.

The entire epibranchial structure is invested in palatal connective tissue. The tissue below the basal part of the organ is produced into four folds (palatal folds of Fang, 1928) which hang down into the interbranchial channels (Figs 25 & 26). The lateral face of the epibranchial organ, also formed from palatal tissue, is connected to the medial face of the preoperculum *via* a segment of the *adductor hyomandibulae* muscle (= *pharyngopraeopercularis* muscle of Zambriborshch, 1955); see Fig. 25.

The morphology of the epibranchial arches in *Hypophthalmichthys* is unique. Modified gill-arches and gill-rakers are, however, found elsewhere in cyprinids. In *Xenocypris argenteus* the epibranchials are rounded over a thickened palatal tissue pad, the gill-rakers are numerous, approximately 25 per 1 mm of gill-arch, and extend to the proximal part of the epibranchial. The infrapharyngobranchials extend into the dorsal surface of the palatal tissue pad. The pads or cushions have a hollow interior, the internal surface of the tissue is highly papillose and convoluted. Similar development of the epibranchials, gill-rakers and palatal cushions are to be found in *Plagiognathops,* although the gill-rakers on the 1st arch are 'normal' and the palatal cushion is more papillose.

An hypothesized plesiomorph condition of the epibranchial organ is encountered in *Abramis.* Here the epibranchials are markedly rounded and the palatal tissue greatly thickened. This is particularly evident in *Abramis sapa* where the palatal cushion occupies a large part of the pharyngeal cavity (Fig. 27b). Anteriorly it is rounded and forms a cup-shaped depression in the palate. The palatal cushion resembles that of *Xenocypris* in having a hollow interior, although not as cavernous. The outer surface of the cushion shows slight ridging between the gill-arches, reminiscent of the palatal folds in *Hypophthalmichthys.* The cartilaginous proximal tips of the epibranchials are highly developed and lie embedded in a cartilaginous casing which extends along the basioccipital (Figs 27a, b). Again, as in

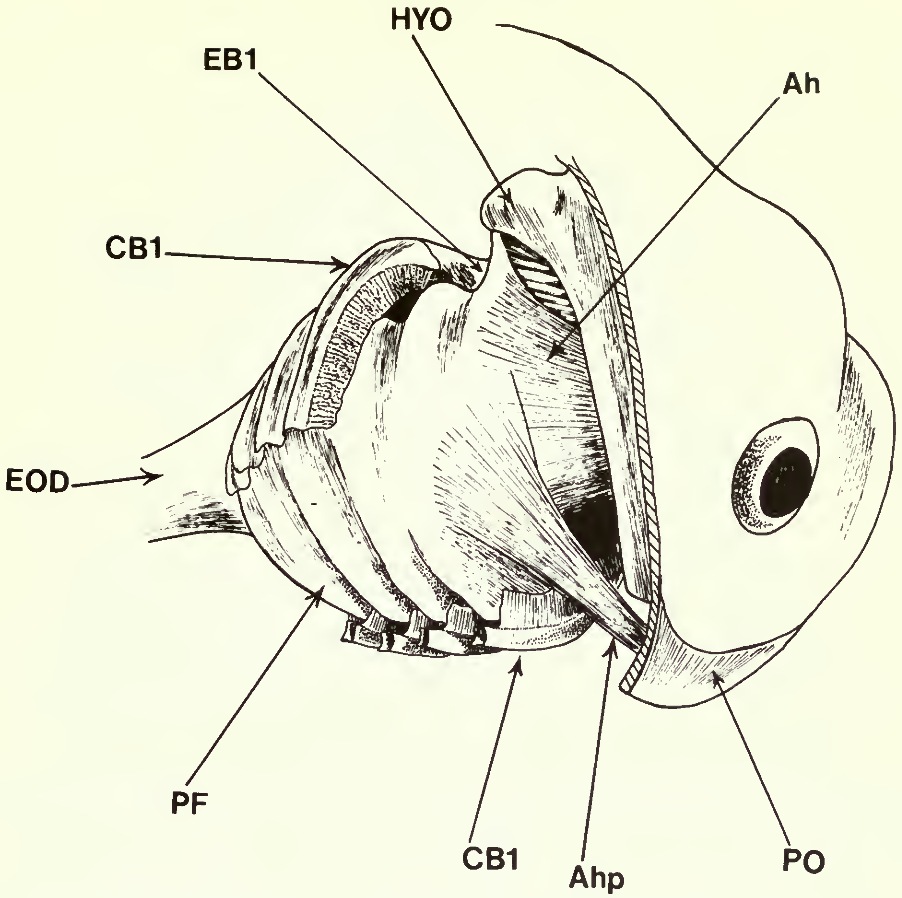


Fig. 25 *Hypophthalmichthys*, postero-lateral view of epibranchial organ and gill-arch elements. The ceratobranchials have been partly cut away to show the organ's folded tissue surface. Schematic drawing based on two dissected specimens.

Xenocypris the cartilaginous tips of the epibranchials extend ventrally into the floor of the palatal cushion roof.

Elsewhere in the Cyprinoidei an epibranchial organ is present in Catostomidae. In these taxa as in *Hypophthalmichthys* and the xenocyprinids, the epibranchials are rounded over a complex pharyngeal pad and are medially prolonged (Fig. 28a). In catostomids the pharyngeal pad more closely resembles that in *Xenocypris* being a medially undivided structure surrounding the basioccipital process, and not in the form of paired diverticula as in *Hypophthalmichthys*. The catostomid basioccipital is expanded laterally and is fretted, playing an integral part in the structure of the pharyngeal cushion. This is unlike the cyprinid condition where the basioccipital acts as a support for connective tissue dividing the organ (see Weisel, 1960 for an account of the catostomid pharyngeal organ, and Eastman, 1977 for a description of catostomid pharyngeal anatomy).

When compared to the epibranchial organs of other teleosts which possess them, that of *Hypophthalmichthys* most closely resembles the continuous tube organs of some clupeids (see Miller, 1969).

It is possible that a form of epibranchial organ occurs in the south-east Asian cyprinid genus *Thynnichthys*. This fish shows a remarkable superficial resemblance to *Hypophthalmichthys*, particularly in its low positioned eye. As in the latter, the gill-arches are elongate but they lack gill-rakers. There does, however, appear to be a swollen area of pharyngeal

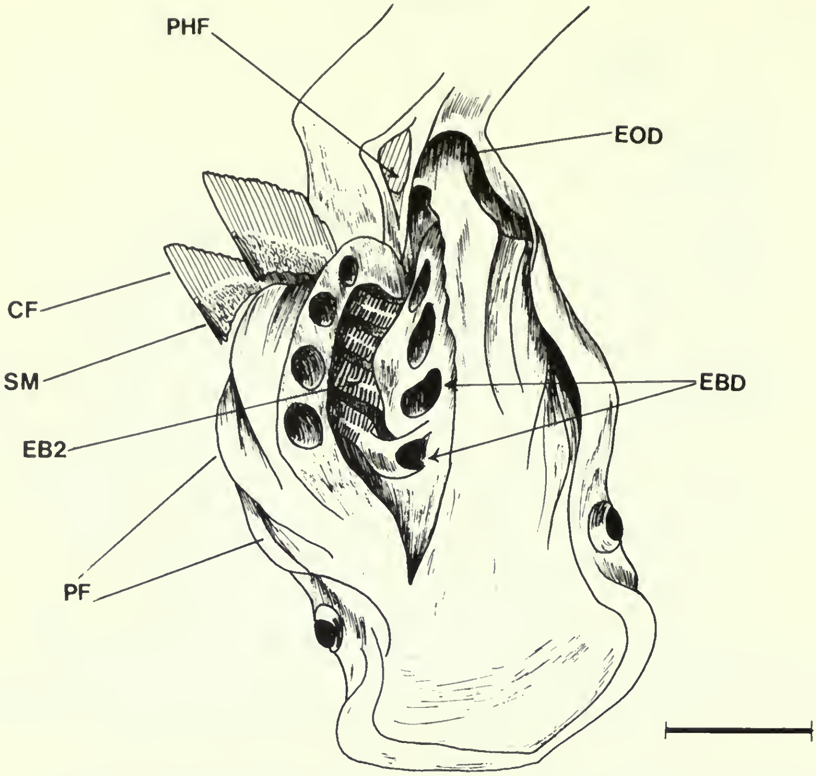


Fig. 26 *Hypophthalmichthys*, ventral dissection of the epibranchial organ, ceratobranchials cut away. Scale = 10 mm. Drawn from specimens BMNH 1895.5.31 : 36–37 and uncatalogued Swinhoe specimen.

tissue with a single posterior median duct leading into the oesophagus. Only a single specimen is available for superficial dissection but those osteological features which are observable are unlike those of *Hypophthalmichthys* and more closely resemble *Amblypharyngodon.*

Although Berry & Low (1970) described certain morphological features in hybrids between *Hypophthalmichthys* and *Ctenopharyngodon*, no mention was made of the development of an epibranchial organ.

A specialization of the upper branchial arch shared by *Hypophthalmichthys* and *Xenocypris* is hypertrophy of the 5th epibranchial. In *Xenocypris* this element is broadly lamellate and has a form of articulation with the 4th ceratobranchial similar to that of *Hypophthalmichthys* (Fig. 28a). In cyprinids the 5th epibranchial is greatly reduced or appears as a small cartilaginous element above the 4th epibranchial (Banister, pers. comm.). The hypertrophy of this element and its articulation with the 4th epibranchial are seen as synapomorphies uniting *Hypophthalmichthys* and *Xenocypris.*

A superficially similar gill-arch morphology to that in *Hypophthalmichthys* occurs in *Gibelion* and *Catlacarpio* (Fig. 28d). In these taxa also the ceratobranchials are elongate and bear numerous gill-rakers. The epibranchials are sickle-shaped, their medial 'handle' portion being dorso-ventrally expanded and antero-posteriorly compressed. The two infrapharyngobranchials are thickened, IF2 being virtually reorientated from the usual horizontal plane to a vertical one. The entire upper branchial basket is surrounded by a thick, papillose pharyngeal cushion and this, together with the fretted basioccipital pharyngeal process greatly resembles the upper pharyngeal anatomy of catostomids. It may be that the catline taxa employ similar feeding methods to those of catostomids (see Weisel, 1960). Again, similarly developed epibranchials are present in '*Labeo*' *stoliczkae* (Fig. 28c), but they are

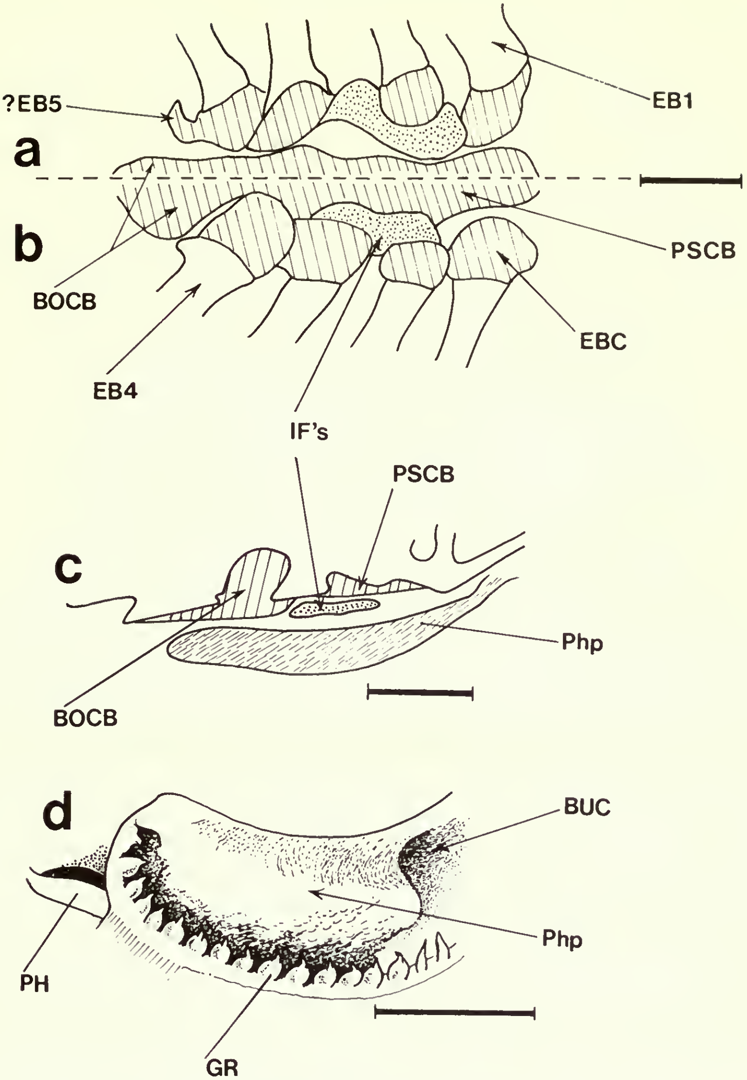


Fig. 27 Upper pharyngeal anatomy of *Abramis.* Dorsal branchial elements of: a. *Abramis brama,* left side BMNH 1974.9.5 : 1–31; b. *Abramis sapa,* right side BMNH 1967.7.17 : 3–4, drawn *in situ,* scale = 1 mm; c. lateral view of cartilaginous basicranial bloc and pharyngeal pad in *A. brama,* scale = 10 mm; d. pharyngeal cavity of *A. sapa* showing 4th ceratobranchial from which most of the gill filaments have been removed, scale = 5 mm.

not so acutely curved medially, and neither are the infrapharyngobranchials orientated in the same way. Furthermore, the basioccipital process is thick and broad. Other neurocranial characters suggest that *'Labeo' stoliczkae* has as its closest relative, *Cirrhina,* whilst *Gibelion* and *Catlacarpio* seem closely related to *Thynnichthys, Amblypharyngodon* and *Osteobrama* (part).

Pharyngeal bones and *teeth* of both genera have been described and figured by Chu (1935). The pharyngeal bone of *Ctenopharyngodon* has a greatly attenuated lower limb and there is a prominent process (for the attachment of the posterior portion of the *levator posterior*) at the curvature of the upper limb. The teeth are in two rows (2, 4–5), greatly compressed and with their grinding surfaces serrate, the serrations being the lateral margins of grooves on the tooth's outer face.

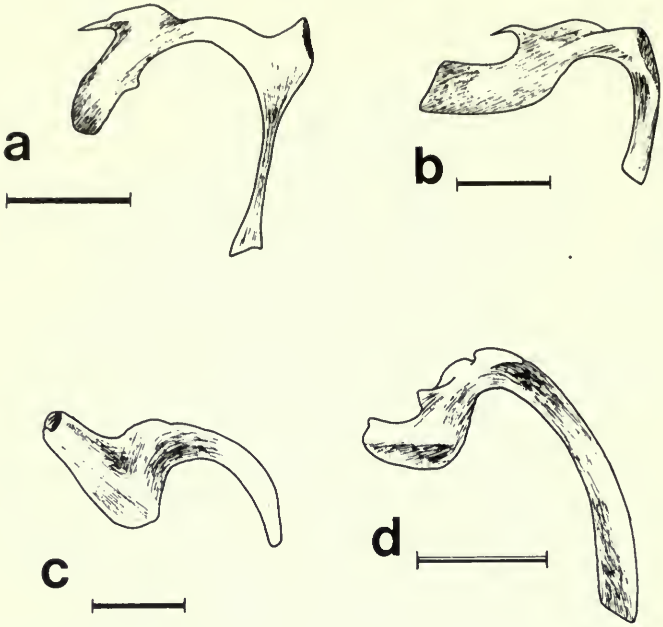


Fig. 28 Posterior views of the right 4th epibranchial of: a. *Xenocypris argenteus* BMNH 1889.6.8 : 19–22 (alizarin); b. *Abramis ballerus* (uncatalogued skeleton); c. *Labeo stoliczkae* BMNH 1891.11.30 : 286 (skeleton); and d. *Gibelion catla* BMNH 1908.12.28 : 1122 (skeleton). Scales for a, b, and c = 2 mm, d = 5 mm.

According to Chu (1935), the teeth and pharyngeal bone of the Hypophthalmichthinae '. . . are singularly unique, without parallel in other cyprinids'. The anterior limb of the pharyngeal bone is dorsoventrally depressed and the upright posterior limb is antero-posteriorly compressed. There is a large fenestra within the expanded dentigerous part of the bone. *In situ* this fenestra is covered laterally by a translucent tissue, medially it serves as a cavity into which the expanded edge of the basioccipital masticatory plate inserts (Fig. 26). The 4 teeth of *Hypophthalmichthys* are in a single row, are compressed, have a concave occlusul surface with a transverse median groove and lateral striation.

Chu (1935) is correct in describing the pharyngeal dentition of *Hypophthalmichthys* as unique. There are, however, similarities between the pharyngeals of this species and those of *Xenocypris* and *Plagiognathops*, where there is also an extensive foramen in the pharyngeal bone, and the teeth have similar grinding surfaces (see Chu, 1935).

21. *Adductor hyomandibulae muscle*

In *Ctenopharyngodon* the *adductor hyomandibulae* is developed as in the majority of cyprinids, namely, a thick dorsal element arising from the face of the prootic and inserting, musculously, on the upper medial face of the hyomandibula.

In *Hypophthalmichthys* the muscle is expanded and is continuous (see below) with the *adductor arcus palatini*, forming a muscular 'wall' which effectively separates the branchial and buccal cavities. The upper part of the muscle (Dahm, Fig. 29) arises from the prootic and inserts on the upper medial face of the hyomandibula as in other cyprinids. However, a posterior segment attaches to the antero-dorsal wall of the epibranchial organ and another part of the (? same segment) of muscle runs from the lateral wall of the epibranchial organ to the preoperculum (*pharyngopraeopercularis* of Zambriborshch, 1955). Anterior to the dorsal part of the muscle another element can be distinguished originating from the lower part of the prootic and the pterosphenoid spur to insert on the medial section of the hyomandibula. Anteriorly this second portion is continuous with the *adductor arcus palatini*

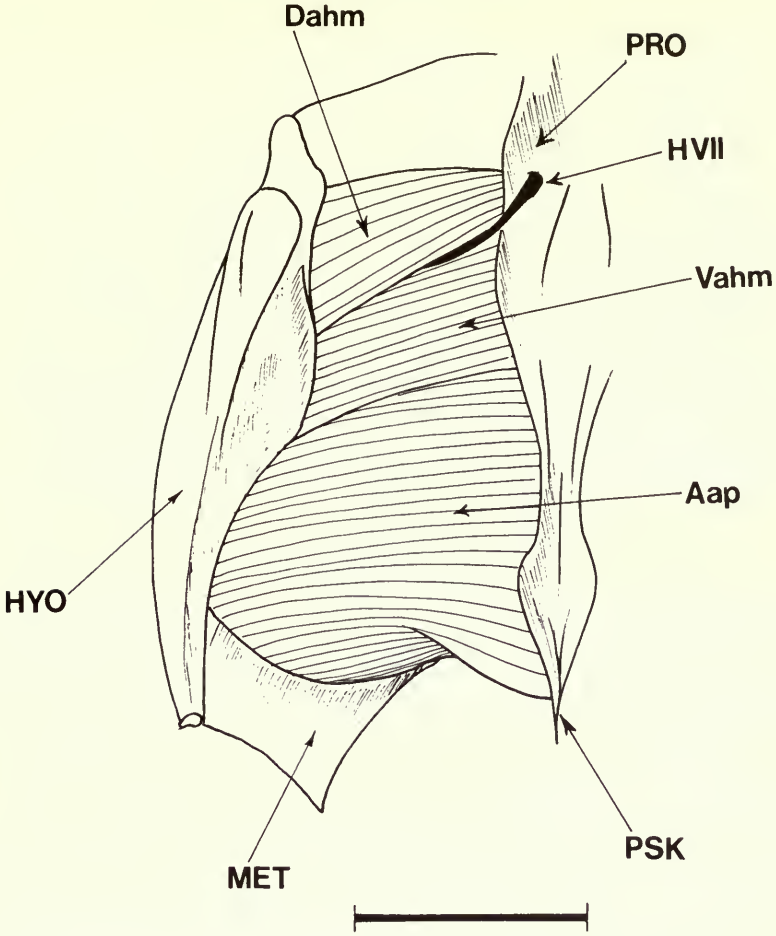


Fig. 29 *Hypophthalmichthys,* ventro-posterior view of *adductor hyomandibularis* musculature, based on specimens BMNH 1895.5.31 : 36–37. Scale = 10 mm.

muscle which originates from the parasphenoid ventral process and inserts along the lower limb of the hyomandibula and, anteriorly, along the dorsal rim of the metapterygoid. Winterbottom (1973) points out that the *adductor hyomandibulae* and, at least in certain taxa, the *adductor arcus palatini* are parts of a single muscle. Certainly, in this case it is only the orientation of the fibres that distinguishes the upper medial section of the muscle as part of the *adductor hyomandibulae* rather than as part of the *adductor arcus palatini.*

Such a highly developed *adductor hyomandibularis* musculature occurs elsewhere only in *Abramis, Rutilus* and *Chondrostoma.* In *Abramis* the upper medial portion of the muscle is strongly attached to the pharyngeal tissue, and thence to the posterior border of the hyomandibula. Although in *Xenocypris* the *adductor hyomandibulae* is not as expansive as in the other genera, the upper medial section is attached, along its entire ventral surface, to the tissue covering the branchial arches, and some fibres appear to extend on to the preoperculum. Morphologically, this can be considered a forerunner of the derived condition realized in *Hypophthalmichthys* where part of the *adductor hyomandibulae* becomes attached to the epibranchial organ and preoperculum and possibly acts as the power unit forcing water through the epibranchial ducts. The *adductor hyomandibulae* morphology in *Hypophthalmichthys, Xenocypris, Abramis, Rutilus* and *Chondrostoma* is considered synapomorphic.

22. *Pectoral girdle*

The pectoral girdle of *Ctenopharyngodon* is remarkably similar to that of *Barbus* and *Cyprinus*, except that the posterior cleithral lamina is extended posteriorly. The horizontal cleithral limb is broad, with a concave anterior border. The cleithra contact each other only at their anterior tips. The coracoid is shallow and rounded posteriorly; the mesocoracoid is narrow.

The pectoral girdle of *Hypophthalmichthys* displays many modifications relative to the presumed plesiomorph pattern. The horizontal cleithral lamina is greatly expanded and rises in the vertical plane to join its partner for the anterior third of its length. The posterior border of the coracoid is square. The mesocoracoid limb is broad. In both genera the postcleithra are elongate and curved mesially, ie. plesiomorphic state; see Howes (1980).

In no other cyprinid is the horizontal cleithral lamina expanded to the same extent as in *Hypophthalmichthys*. Only in *Abramis* and *Xenocypris* is there an approachable condition. In these taxa, however, the medial cleithral border is deeply notched at a point just below the dorsal articulation of the mesocoracoid. The function of this notch is to contain the expanded border of the pharyngeal bone. The mesocoracoid limb is broad in all these taxa.

Phylogenetic relationships

From the foregoing descriptions and analyses of *Ctenopharyngodon* and *Hypophthalmichthys*, a series of apomorph characters can be identified, none of which is shared by both taxa. Instead, these characters serve to relate the respective genera to other taxa and thus *Ctenopharyngodon* and *Hypophthalmichthys* must be considered members of two distinct monophyletic assemblages.

Relationships of *Ctenopharyngodon*

The following characters are identified as apomorphies.

1. Subtemporal fossa extending anteriorly to invade the autosphenotic on which part of the pharyngeal musculature originates (p. 15)
2. Lateral notch in the supraethmoid with which the palatine head articulates (p. 5)
3. Extensive prootic with ventrally directed trigemino-facialis foramen (p. 13)
4. Extensive intercalar forming posterior corner of cranium and contributing to an accessory subtemporal fossa (p. 22)
5. Divided *levator posterior* muscle, the posterior segment originating from the intercalar (p. 22)
6. Extensive and bullate epioccipital (p. 21)
7. Reduced lateral occipital fenestra (p. 21)
8. Olfactory foramen countersunk entirely within the lateral ethmoid (p. 9)
9. Frontal broad and sloping ventrally (p. 18)
10. Massive and shelved supraorbital (p. 20)
11. Orbital portion of parasphenoid broadened and with ventral ridge (p. 11)
12. Ventrally directed pterosphenoid process (p. 10)
13. Thickened 1st infraorbital (p. 20)
14. Distally broadened and upwardly curved basioccipital pharyngeal process (p. 23)

Characters 1–6 are synapomorphies with *Mylopharyngodon* and *Squaliobarbus*; 7–11 with *Mylopharyngodon*; 12–14 are autapomorphic.

From the distribution of these apomorph characters, *Mylopharyngodon* is considered to be the sister taxon of *Ctenopharyngodon* with both forming the derived sister group of *Squaliobarbus*. These three taxa constitute a monophyletic lineage termed the *Squaliobarbine group*.

Mylopharyngodon (Fig. 30b) is a monotypic genus (type species *M. piceus* (Richardson, 1845)), characterized by the autapomorphic features of an extensive bowl-like masticatory

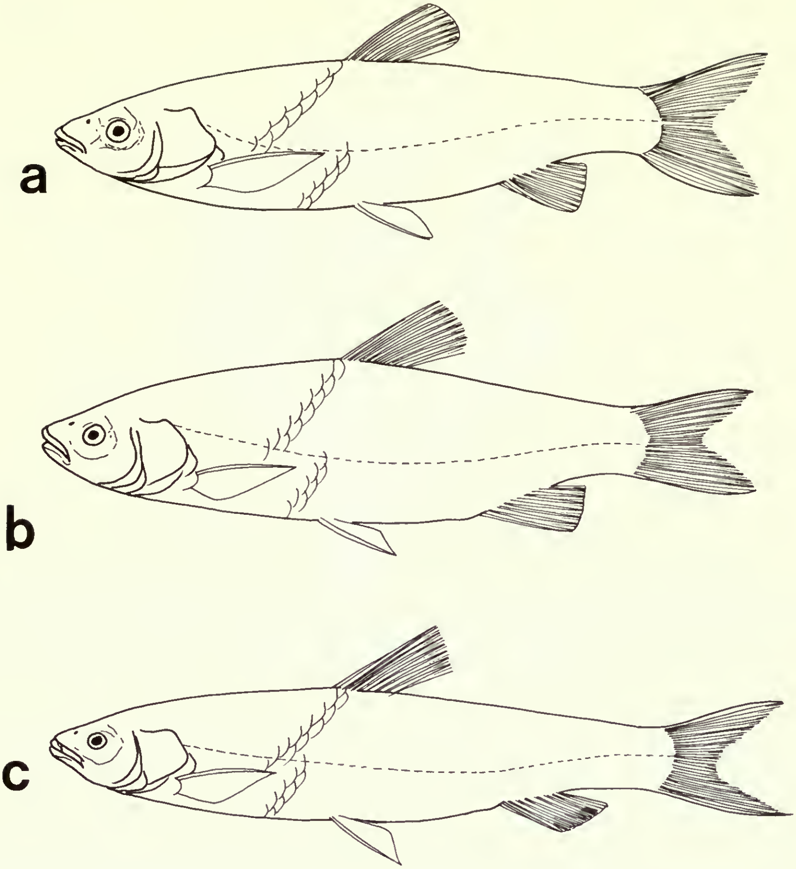


Fig. 30 Outline drawings of members of the *squaliobarbine group*: a. *Ctenopharyngodon idellus*; b. *Mylopharyngodon piceus*; and c. *Squaliobarbus curriculus*.

plate (Fig. 19b); large molariform pharyngeal teeth; small basioccipital facet dorsally overlapped by an exoccipital ridge (Fig. 31); and narrow, mesially curved posterior cleithral lamina.

Squaliobarbus (Fig. 30c) is the plesiomorph member of the lineage differing from its sister taxa in possessing two pairs of small barbels. The anterior pair of barbels are minute and appear superficially as mere appendages of the ventral infraorbital skin fold. However, the barbel is innervated by a sub-branch of the VII facial nerve. The main nerve branch passes through a foramen in the maxilla just below a shelf which forms the attachment point of the palatine ligament. The barbel originates some distance posterior to the maxillary foramen and the main nerve branch supplies the lip fold.

It was stated on p. 28 that a maxillary foramen carrying a nerve supply to an anterior barbel is an apomorph character uniting those taxa which possess it. It was also noted (p. 28) that *Ctenopharyngodon* has a maxillary foramen but both nerve and barbel are lacking. In *Mylopharyngodon* there is no trace of a maxillary foramen or barbels.

Two hypotheses are proposed to account for the distribution of barbels and associated foramina amongst squaliobarbines:

1. That *Ctenopharyngodon* and *Mylopharyngodon* represent a plesiomorph condition in which the foramen and/or barbel has not formed.
2. That the absence of barbels and associated nerve in these genera represents secondary losses.

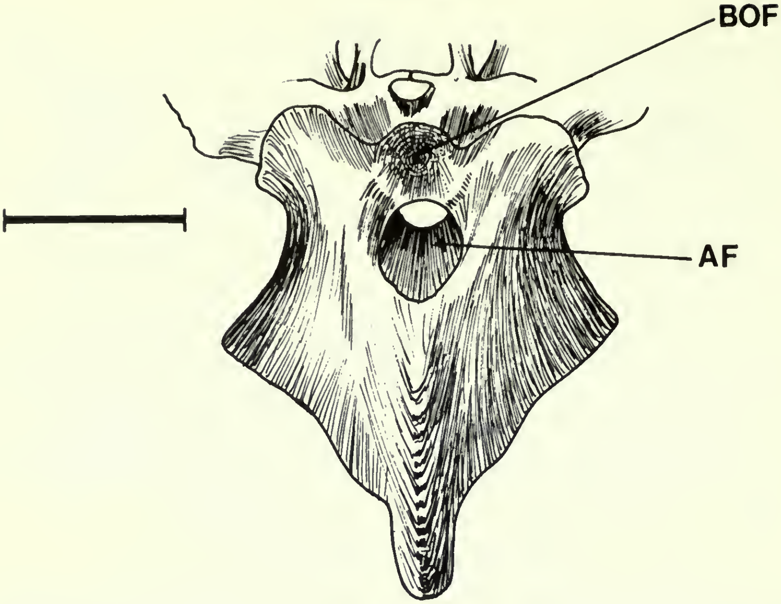


Fig. 31 *Mylopharyngodon piceus*; posterior view of basioccipital from specimen BMNH 1895.5.31 : 40. Scale = 5 mm.

It is assumed that the second hypothesis is more likely to be the correct one as the plesiomorph lineage (*Squaliobarbus*) possesses barbels, and that in this taxon their reduction and that of the associated nerve signifies transition to loss state. Also, reduction of barbels is recorded in other cyprinid taxa (see Banister & Bunni, 1980).

The distribution of cyprinid barbels; anterior and posterior, whether they are associated with a foramen, the type of nerve supply and form of proximal attachment is a subject dealt with elsewhere (Banister & Howes, in preparation). For the purposes of this discussion it is considered that the squaliobarbine assemblage form part of that series of taxa which possess a maxillary foramen carrying a nerve supply to an anterior barbel.

The suite of apomorph characters defining the squaliobarbines involves, for the most part, the occipital region of the cranium—the expansion of the subtemporal fossa and the intercalar. These osteological features are concomitant with an increased evolutionary development of the *levator posterior* muscle which extended forward into the autosphenotic and was divided posteriorly, the posterior section originating from the intercalar. These specializations could be associated with the essentially phtyophagous habits of the squaliobarbine taxa.

The proposed theory of relationships is to regard the squaliobarbine group as a divergently specialized sister lineage to all other barbelled Cyprinidae (i.e. Cyprininae); see Fig. 32.

Synopsis of taxa assigned to the Squaliobarbine group

Ctenopharyngodon Steindachner, 1866

Pristiodon Dybowskii, 1877

Type and only species: *C. idella* (Valenciennes, 1844).
Distribution: Pacific drainage of the USSR and China, lat. 50°–23°N.
Introduced into many tropical and temperate areas including Europe, North America, India, New Zealand, Malaysia.
Principal bibliographic sources concerning biology: Lin, 1935; Nikolsky, 1954; Inaba & Nomura, 1956; Hickling, 1967; Okada, 1960; Cross, 1969; Edwards, 1974.

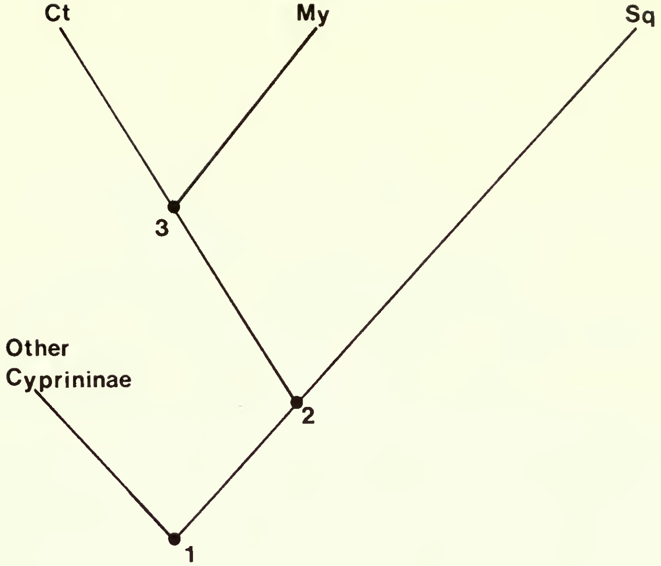


Fig. 32 Cladogram representing the phyletic relationships of the *squaliobarbine group.* Ct = *Ctenopharyngodon,* My = *Mylopharyngodon,* Sq = *Squaliobarbus.* Node 1. Possession of maxillary foramen. Node 2. Synapomorphies 1–7 (page 38). Node 3. Synapomorphies 8–11 (page 38), also loss of maxillary foramen in *Mylopharyngodon.*

Mylopharyngodon Peters, 1873

Myloleucus Günther, 1873
Myloleuciscus Garman, 1912
Leucisculus Oshima, 1920

Type and only species: *M. piceus* (Richardson, 1845).
Distribution: Amur, China, Formosa.
Principal bibliographic sources: Nikolsky, 1954 & 1956.

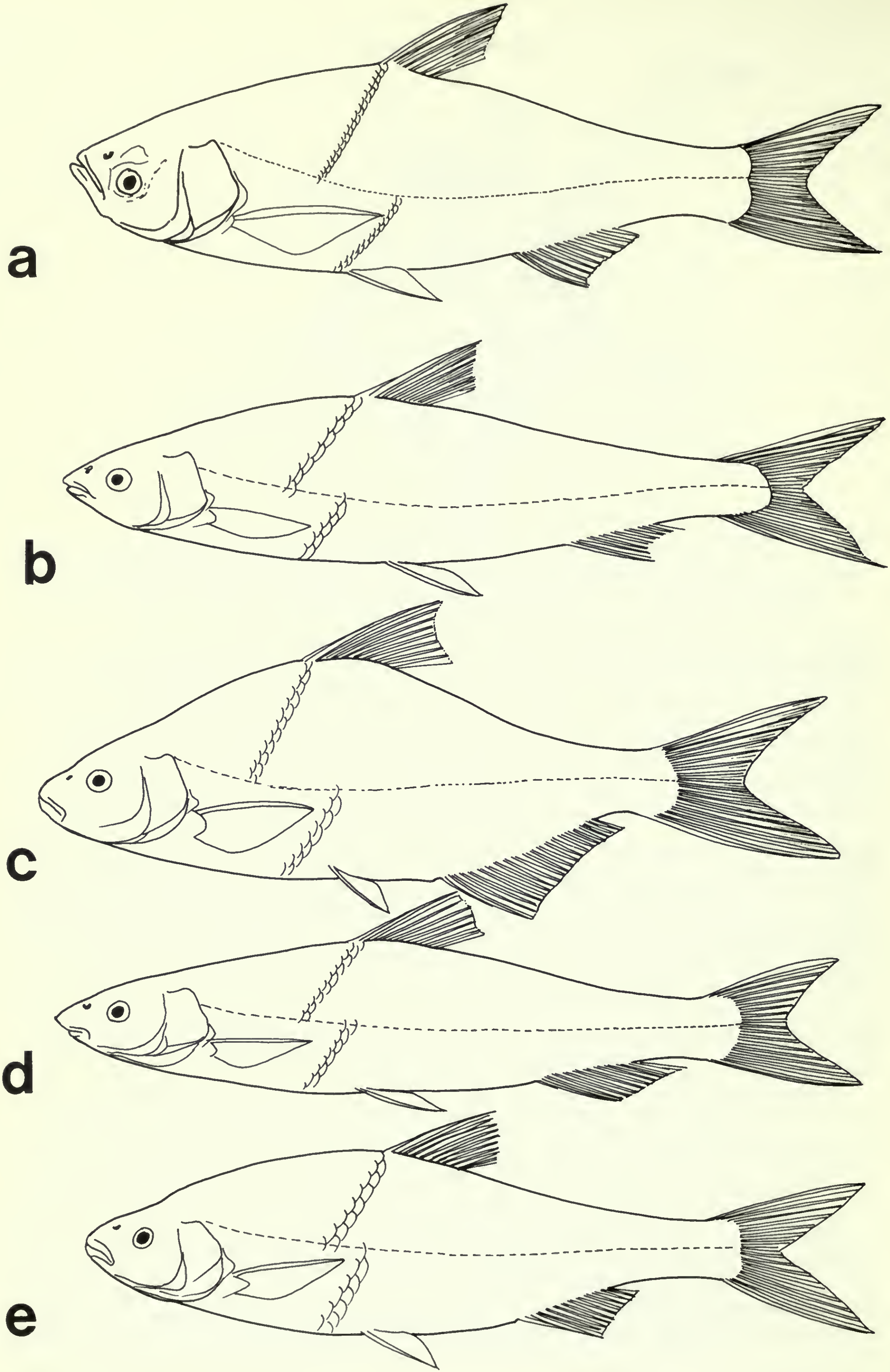
Squaliobarbus Günther, 1868

Type species: *S. curriculus* (Richardson, 1845).
Sauvage (1884) described another species, *S. caudalis,* from Tonkin. Pellegrin (1934), when commenting on the Hanoi collection of Sauvage, made no mention of this species but included in his list, *S. curriculus.*
Distribution: Amur, China, Western Korea, Hanoi.
Principal bibliographic source: Nikolsky, 1956.

Relationships of *Hypophthalmichthys*

The following characters are identified as apomorphies:

1. Medial ethmoid notch floored by the vomer (p. 9)
2. Frontal with an acute lateral slope, providing an extensive cranial dilatator fossa (p. 15)
3. Extensive lateral occipital fenestra (p. 21)
4. Modification of the *adductor hyomandibulae* muscle involving partial attachment to the preoperculum and upper pharyngeal tissue (p. 36)
5. Expanded horizontal cleithral lamina (p. 38)
6. Markedly rounded epibranchials (p. 33)
7. Deep basioccipital keel with marked concave anterior border (p. 23)
8. Carotid foramen contained in ventrally produced parasphenoid process (p. 12)
9. Lateral ethmoid-frontal fenestra (p. 9)
10. Expanded 1st and 4th epibranchials, the 5th present and hypertrophied (p. 34)


a
b
c
d
e

11. Extensive fossa in pharyngeal bone (p. 36)
12. Exoccipital wing extended distally to contact pterotic spine (p. 21)
13. Curved posttemporal (p. 25)
14. Pterosphenoid contributing to anterior trigemino-facialis foramen (p. 10)
15. Cardiform masticatory plate with tubular posterior extension (p. 23)
16. Intercalar invading border of exoccipital (p. 22)
17. Complexly developed epibranchial organ (p. 31)
18. Neural complex bifurcated and articulating with supraoccipital (p. 30)

Characters 1–6 are synapomorphic with *Abramis* and *Xenocypris* (?*Plagiognathops* and *Distoechodon*); 7–13 with *Xenocypris*; 14–18 are autapomorphic.

From the distribution of these apomorph characters *Xenocypris* is regarded as the twin taxon to *Hypophthalmichthys.* Together they form the sister group to an assemblage including *Abramis.*

Xenocypris (Fig. 33b). The taxonomy of this genus is confused, two other monotypic taxa, *Plagiognathops* and *Distoechodon* being regarded by some authors as subgenera (see Bănărescu, 1970). All these taxa are presently placed in the subfamily Xenocyprinidinae.

Two previous comments regarding *Xenocypris* are in need of modification. The first (Howes, 1979), was to the effect that the Xenocyprinidinae was polyphyletic, *viz* that the included genera, *Xenocypris, Plagiognathops* and *Distoechodon* shared no derived characters. In fact they do (see below). The second statement (Howes, 1980) was that the closest relatives of *Xenocypris* are amongst the hemicultrines (*Hemiculter, Hemiculterella* and *Ochetobius*). This assumption was based on what are now deemed to be symplesiomorphies, and indeed, the hemicultrines as earlier conceived represent a paraphyletic assemblage.

Plagiognathops and *Distoechodon* share with *Xenocypris* (as represented by the type species *X. argenteus*) apomorph characters involving the gill-arches and basioccipital, although they are not so highly derived as in *Xenocypris.* Lack of osteological material prevents a complex diagnosis of the character complexes and the three genera are considered together as an unresolved trichotomy.

Abramis (Fig. 33c), here including the 'genera' *Vimba* and *Blicca*; see p. 46, shares with *Xenocypris* and *Hypophthalmichthys* synapomorphic characters 1–6, involving the ethmoid region, cranial roof, pharyngeal roof covering and associated musculature. However, a simple sister-group relationship between *Abramis* and *Xenocypris* + *Hypophthalmichthys* is doubtful in the light of other apomorphies possessed by *Abramis* and exclusively shared with *Chondrostoma* and *Rutilus* (Figs 33d & e). These are:

(i) confluent ventral channelling of the parasphenoid and basioccipital;
(ii) columnar, dorsally bifurcated neural complex; and
(iii) gill-rakers with globular, papillate bases.

The underlying synapomorphy (Saether, 1979) uniting *Rutilus, Chondrostoma, Abramis,* the *Xenocypris* complex and *Hypophthalmichthys* is a modification of the basicranium, *viz* a parasphenoid notch or confluent ventral channelling of the parasphenoid and basioccipital, and deepening of the basioccipital process. From the distribution of synapomorphies within this assemblage—termed the *Abramine group*—two hypotheses of generic relationships are available and represented as cladograms A & B (Fig. 34).

In cladogram A, *Abramis* is reckoned to be the sister group of *Rutilus* and *Chondrostoma* (the similarity between the parasphenoid-basioccipital morphology links these two genera as sister taxa) on the basis of characters (i) and (ii) cited above. In this case, the characters *Abramis* shares with *Hypophthalmichthys* and the *Xenocypris* complex (listed as synapomorphies 1–6 on p. 41) must be considered as convergent.

In cladogram B, *Abramis* is considered as the sister group to *Hypophthalmichthys* + the

Fig. 33 Outline drawings of members of the *abramine group*: a. *Hypophthalmichthys molitrix*; b. *Xenocypris argenteus*; c. *Abramis brama*; d. *Chondrostoma nasus*; e. *Rutilus rutilus.*

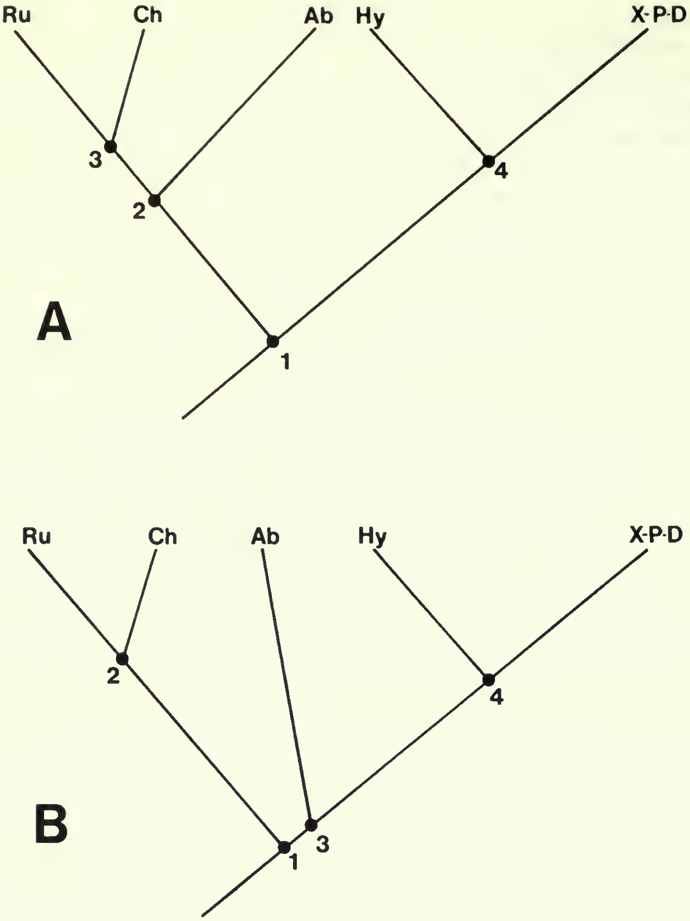


Fig. 34 Cladograms expressing two schemes of phyletic relationships of the *abramine group*. Ru = *Rutilus*, Ch = *Chondrostoma*, Ab = *Abramis*, Hy = *Hypophthalmichthys*, X-P-D = *Xenocypris-Plagiognathops-Distoechodon* trichotomy.
Cladogram A. Node 1. Modification of basioccipital-parasphenoid; development of pharyngeal pad; transversely convex vomer; hypertrophy of *adductor hyomandibulae* muscles. Node 2. Basioccipital-parasphenoid channel; columnar neural complex; globular based gill-rakers. (Convergence of 6 characters in *Abramis* with *Hypophthalmichthys* and *Xenocypris*.) Node 3. Synapomorphic basioccipital morphology (see Fig. 18). Node 4. Synapomorphic gill-arch structure; development of epibranchial organ and associated basicranial deepening. (Loss of convex vomer and deep ethmoid in *Hypophthalmichthys*.)
Cladogram B. Node 1. Combination of nodes 1 and 2 in cladogram A. Node 2.= node 3 in cladogram A. Node 3. Synapomorphies 1–6 (p. 41). Node 4. Synapomorphies 7–13 (p. 41); also loss of 5 characters through nodes 1–3 (see text, p. 43).

Xenocypris complex. In this case, five characters must be recognized as having been secondarily lost in the two latter taxa, *viz*: parasphenoid-basioccipital channel; columnar neural complex; globular based gill-rakers (lost in both *Hypophthalmichthys* and *Xenocypris*); convex and deeply notched ethmoid (lost in *Hypophthalmichthys*).

It may be argued that in their vertebral elements *Hypophthalmichthys* and *Xenocypris* are conservative and have retained the plesiomorphic lamellate neural complex. Likewise, *Hypophthalmichthys* may have retained the plesiomorphic ethmo-vomerine bloc. (No evidence is available to show that apomorphic modifications of the ethmoid region are linked with those of the basicranium.) If this is so, then the more likely hypothesis is that

Rutilus, Chondrostoma and *Abramis* form the sister group to *Hypophthalmichthys* and the *Xenocypris* complex, as one has only to postulate the loss of the apomorphic ethmovomerine assembly in *Hypophthalmichthys* (cladogram A). This is also the more likely hypothesis of relationships if the autapomorphic parasphenoid-basioccipital and neural complex of *Abramis* are seen as terminal points of a possible evolutionary sequence represented by the more plesiomorphic types in *Rutilus* and *Chondrostoma.*

Although it may appear that *Abramis* displays an incipient form of the epibranchial structure in *Xenocypris,* this is misleading. In fact, the gill-arch morphology and pharyngeal dentition suggests that the pharyngeal pad of *Abramis* differs functionally from that of *Xenocypris* and its relatives. There is indeed, no 'morphoclinal' or 'transitional' series represented in extant abramine genera which might reflect the evolutionary development of an epibranchial organ. However, the basic architectural modification of the basicranium (deepening of the parasphenoid and basioccipital) can be seen as a preadaptation to the formation of an epibranchial structure which in the abramines appears to have followed two evolutionary pathways hypothesized to be most closely represented by the relationships expressed in cladogram A. Falsification of either hypothesis will be forthcoming when more complete anatomical data are available for *Plagiognathops* and *Distoechodon* and a functional analysis of pharyngeal/epibranchial mechanisms available for all abramine taxa.

Synopsis of taxa assigned to the Abramine group

Hypophthalmichthys Bleeker, 1860

Cephalus Basilewsky, 1855
Abramocephalus Steindachner, 1869
Onychodon Dybowski, 1872
Aristichthys Oshima, 1915

Type species: *H. molitrix* (Valenciennes, 1844).
Two other species, *H. nobilis* (Richardson, 1844) and *H. harmandi* Sauvage, 1884 are included. Reasons have already been given for synonymizing *Aristichthys* (p. 2)
Distribution: Amur, China. Introduced into Taiwan, Thailand, Japan, Sri-Lanka, Europe and North America.
Principal bibliographic sources concerning biology: Tsui, 1936; Nikolsky, 1956.

Xenocypris Günther, 1868

Type species: *X. argentea* Günther, 1868.
Another 9 or 10 species are recognized by various authors; see Bănărescu (1970) for most recent revision, and Nikolsky (1956) for biological data.

Plagiognathops Berg, 1907

Type and only species: *P. microlepis* (Bleeker, 1871).
Distribution: Yangtze, middle Amur, Ussuri, Lake Khanka (see Berg, 1949).

Distoechodon Peters, 1880

Type and only species: *D. tumirostris* Peters, 1880.
Distribution: Southern China.

Rutilus Rafinesque, 1820

Scardinius Bonaparte, 1837
Hegerius Bonaparte, 1845
Acanthobrama Heckel, 1843
Leucos Heckel, 1843
Pigus Bonaparte, 1845
Cenisophius Bonaparte, 1845
Gardanus Bonaparte, 1845

Pararutilus Bonaparte, 1845
Pachychilon Steindachner, 1866
Rubellus Fitzinger, 1873
Mirogrex Goren, Fishelson & Trewavas, 1973

Type species: *R. rutilus* Rafinesque, 1820.
Numerous nominal species with a wide distribution throughout Europe, USSR, Israel to the Tigris and Euphrates.

The characters used to define Leuciscine genera are criticized below (p. 48). Typical are the use of modal numbers of fin rays, lateral line scales, gill-rakers and plesiomorphically low vertebral counts. No comparisons of the osteology of the various 'genera' given in the above synonymy have been made previously. I have compared the osteology of *Rutilus rutilus* with a selection of species currently assigned to this genus, to *Scardinius,* to *Acanthobrama* and to *Mirogrex* and am unable to find any noticeable differences. Indeed, all these taxa possess those apomorph characters which identify *Rutilus, viz* form of the median ethmoid notch; extension of the vomerine arms; preethmoid not, or barely contacting the mesethmoid; columnar neural complex; globular, papillate based gill-rakers.

Scardinus is usually separated from *Rutilus* on the basis of its having the pharyngeal teeth in two rows instead of a single row, and the presence of a ventral body keel. I would consider that the differences in pharyngeal teeth are of a specific nature, as in *Abramis* (see Shutov, 1967 and Eastman & Underhill, 1973); likewise, the ventral keel is variously developed in *Rutilus rutilus.* Wheeler (1976) concluded that of the features used to characterize *Rutilus* and *Scardinius* the morphology of the pharyngeal teeth was probably the most significant. If Chu's (1935) hypothesis is accepted, namely that three rows of pharyngeal teeth represent the primitive (plesiomorph) condition, then the two rows of *Rutilus* and the single row of *Scardinius* are seen as successively derived states. In the majority of *Rutilus* × *'Scardinius'* hybrids a second tooth row is apparent which may indicate a dominant genetical pattern for the plesiomorph condition.

Concerning the synonymy of *Acanthobrama* and *Mirogrex*; Goren, Fishelson & Trewavas (1973) separate these two genera on modal differences in the number of lateral line scales, gill-raker counts and the number of vertebrae. These authors compare the two 'genera' with *Capoetobrama* (see below), but not with *Rutilus,* and they state that the generic position of the presumed ancestral taxon to *Acanthobrama, 'Rutilus' tricolor* '... has not been determined'. I would agree that the species *tricolor* does not belong to *Rutilus* and should properly be placed amongst a complex including *Leucaspius.* However, *Acanthobrama* and *Mirogrex* share all the apomorph characters of *Rutilus sensu stricto,* they are thus to be regarded as belonging to that genus. The genus *Capoetobrama* (see above) does not belong to this assemblage at all and may be more closely allied to the alburnine group (unpublished obs.).

Abramis Cuvier, 1817

Ballerus Heckel, 1843
Blicca Heckel, 1843
Zopa Fitzinger, 1873
Vimba Fitzinger, 1879
Leucabramis Smitt, 1895
Sapa Kazanskii, 1928

Type species: *A. brama* (Linnaeus, 1758).
Five or six species with wide distribution in Europe, the Baltic, Black, Aral and Caspian seas; Asia Minor, Caucasus.
Principal bibliographic source: Backiel & Zawisza, 1968.

Shutov (1969) considered *Blicca* synonymous with *Abramis.* His analysis of populations of *Blicca bjoerkna* revealed a morphometric range encompassing that of *Abramis brama* and a decrease in the numbers of teeth in, and ultimate loss of the second tooth row across the range of the samples. Similarly, I find no differences in the osteology of *Abramis* and *Vimba.*

Both genera possess an identical form of parasphenoid-basioccipital border with ventral channel and notch and highly developed pharyngeal tissue pads. They also share the apomorphic feature of a scaleless pre-dorsal fin ridge. Characters formerly used to separate these 'genera', such as the position of the anal fin origin and the presence of a dorsal ridge on the caudal peduncle are continuously variable and meaningless as taxon defining criteria. All *Abramis* species display considerable morphometric variability (see Berg, 1949 and Bănărescu, 1963).

Chondrostoma Agassiz, 1835

Type species *C. nasus* Agassiz, 1835.
Berg (1949) records 18 species, having a wide distribution throughout Europe south to the Tigris and Euphrates.

Chondrostoma is characterized by those autapomorphic characters associated with forshortening and deepening of the upper jaw bones and a forwardly inclined coronoid process on the dentary. The posterior extension of the pharyngeal plate is thin and broad with a grooved dorsal surface. Assertions made concerning *Chondrostoma* in the anatomical descriptions presented here refer only to the type species, *C. nasus.*

Discussion

Earlier comments (Howes, 1976) that few, if any, presently recognized cyprinid subfamilies are monophyletic (in the sense of Hennig, 1966) have been amply reinforced by this study. Two genera, *Ctenopharyngodon* and *Hypophthalmichthys* previously included in the Leuciscinae are here identified as representative of two monophyletic lineages only distantly related.

As noted above (p. 28), the presence of a maxillary foramen (or its suggested past presence) associated with a rostral barbel is considered apomorphic for one branch of a diphyletic division of the Cyprinidae. It is to this assemblage that the monophyletic lineage (squaliobarbine group) containing *Ctenopharyngodon* belongs. *Hypophthalmichthys* is contained within the abramine group and belongs to that assemblage of taxa lacking the maxillary foramen. It is the majority of these taxa which are provisionally recognized as the subfamily Leuciscinae.

Nikolsky (1954) made a similar dichotomous classification of the Cyprinidae. In one branch he included leuciscines, *Aspius* '. . . and other fish', the other he represented by *Barbus, Cyprinus* and *Gobio.* Nikolsky did not give formal recognition to these divisions and retained the formerly recognized subfamilies without assigning them to one or other lineage.

The following discussion is concerned mainly with the classification and intrarelationships of the non-barbelled cyprinids (Leuciscinae).

Classification of the Leuciscinae

The 'subfamily' Leuciscinae (originally a division introduced by Bonaparte, 1846) has long been used as a category for containing 'generalized' cyprinids, including approximately 40% of Old-World genera. Not all authors have accepted the Leuciscinae; Berg (1949) assigned the majority of Old-World genera to the Cyprininae. On the other hand, Hubbs & Lagler (1958) extended the geographical range of the Leuciscinae to embrace New-World genera. Gosline's (1978) concept of the Leuciscinae embraced also the Cultrinae. These decisions demonstrate a lack of methodology in determining cyprinid supraspecific relationships.

As it stands, the Leuciscinae includes at least four monophyletic assemblages; aspinine (Howes, 1978), abramine (reported herein), alburnine and phoxinine (unpublished) all of which are interrelated to other non-barbelled cyprinids presently recognized as four monophyletic lineages; bariliine (Howes, 1980), cheline (Howes, 1979), hemicultrine (Howes, 1978, part) and cultrine (Howes, 1978, part). It seems, however, that none of these groups is a likely candidate for the status of sister-group to the abramines.

Identification of the abramine sister-group is hampered by the non-resolution of the monophyly of the nucleus of the Leuciscinae, the genus *Leuciscus*. It appears that part of *Leuciscus* is related to the aspinine group and another possibly forms the sister-group to the abramines. Characters supporting an abramine-*Leuciscus* relationship are the presence in some species of *Leuciscus* of an incipient ventral basioccipital channel and a similarity in the ethmovomerine region.

Abramis has been thought by some authors to be related to the American cyprinid genus *Notemigonus* (Miller, 1958 : 203; Bănărescu, 1973). Contrary to this idea I find no synapomorphies linking *Notemigonus* to any member of the abramine group. At this point it must be stated that New-World Cyprinidae have not been surveyed in depth in an attempt to formulate their relationships with any element of the Old-World Leuciscinae. Only *Ptychocheilus* has been examined in detail and would seem (together possibly with *Algansea*) to share apomorphies with the Old-World aspinine group (work in preparation). Whilst it may well be that New-World genera such as *Notropis* and *Chrosomus* are closely related to the Eurasian *Phoxinus* (see Mahy, 1975), it is quite wrong to consider them as synonymous (Bănărescu, 1973). It must be borne in mind that *Phoxinus* as it stands is also a paraphyletic group and such is likely to be the status of *Chrosomus* and *Notropis*.

Christopher & Linder (1979) note the close similarity between *Chondrostoma* and the American *Acrocheilus*. Certainly the jaw morphology of both taxa are alike but no other cranial features demonstrate a close relationship.

At some level, of course, the New-World cyprinids must form sister groups of the Old-World. Whether they represent a single monophyletic sister group to one or other of the monophyletic lineages contained within the 'Leuciscinae' or comprise several lineages forming twin taxa with other non-barbelled Old-World groups (cultrines, chelines, etc) are theories which remain to be tested.

Leuciscine hybrids

Futuyama (1979) notes that '. . . typological thinking focuses first on the "pure" forms and then interprets intermediate phenotypes as secondary products. If we focused on the continuum of phenotypes as a unit, we might not worry as much about which are the species and which the hybrids'.

Futuyama's statement is supported by a revised concept of leuciscine genera. Former hypotheses for the relationships between leuciscine genera have depended upon degree of genetic compatibility as demonstrated by hybridization. The measure of relationship being determined by terminal development stage of offspring, survival rate and reproductive viability. A contrary opinion regarding the validity of hybridization in a phylogenetic context has been expressed by Rosen (1979). Rosen regards reproductive compatibility as a plesiomorphy marked by mosaic distribution within a group. This hypothesis would certainly account for those conflicting cases amongst cyprinids where supposedly phylogenetically closely related taxa fail and distantly related ones succeed in being reproductively compatible. Such inconsistencies are usually explained away as misidentification of parental stocks. Suzuki's (1968) explanation for one such conflicting result was that '. . . Some Soviet species of Leuciscinae are probably more closely related to Cyprininae than Japanese species of Leuciscinae'. Such a statement disregards any kind of rigorous methodology in elucidating phylogenetic relationships.

A greater number of *naturally* occurring *intergeneric hybrids* have been reported for Leuciscine genera than for possibly any other group of teleosts (see Schwartz, 1972). A more rigorous (cladistic) definition of these genera reduces many cases of *intergeneric* to *interspecific* hybridization (ie. crosses between *'Vimba' 'Blicca'* × *Abramis* (Berg, 1949), *'Aristichthys'* × *Hypophthalmichthys* (Voropayev, 1969), *'Scardinius'* × *Rutilus* (many reports, see Schwartz, 1972). Naturally occurring intergeneric hybrids are judged to be so on the basis of intermediacy of characters, notably the pharyngeal dentition. A typical example of the use of 'intermediate' characters is given by Berg (1949 : 88–89) for a 'hybrid' population of *Leuciscus cephalus* × *Chalcaburnus chalcoides*. As enumerated, these characters could well describe a populational variant of one of the presumed parental species.

A similar argument can be applied to many so-called *interspecific hybrids*. The likelihood is that they are not crosses but clinal or other populational fragments. The numerous subspecies and varieties described in Leuciscine genera by Berg (1949) indicate a considerable degree of populational variability. This of course is not to deny that interspecific hybridization does occur.

Wheeler (1976) notes that high levels of hybridization amongst cyprinid taxa occur in areas where recent introductions have been made. Certainly, nearly all the records I have checked for 'intergeneric' European cyprinid hybrids have been cases involving one or both of the taxa being recently introduced into a 'new' ecological situation.

I conclude that 'hybridization' amongst cyprinid taxa must be treated with caution and is a useless character as a measure of phylogenetic affinity.

Classification of the 'true' carps

The squaliobarbine group belongs to the great assemblage of taxa characterized by the presence of a maxillary foramen and (usually) an associated rostral barbel (see p. 28). As yet no accounts of monophyletic groups, other than the squaliobarbines (dealt with herein), have been published, although Reid (1978, unpublished thesis) has identified a labeoine group. The hypothesis proposed above (p. 40) that the squaliobarbines form the sister group to all other barbelled carps is a temporary expedient. But, with available data I am unable to offer a more worthwhile solution. Such genera as *Capoeta, Cyprinus* and *Carassius* appear to be more closely related to the squaliobarbines than do other investigated taxa. Work in preparation (Banister & Howes) seeks to establish monophyletic grouping amongst the barbelled cyprinids. In view of the suspected non-monophyly of so many currently recognized cyprinid assemblages, the reconstruction of ichthyogeographical relationships (eg. Bănărescu, 1973) is fruitless.

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Morphology and systematics of some interior-walled cheilostome Bryozoa

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Synopsis

The colony structure and zoodial morphology found in two cryptocystidean cheilostome bryozoan Families, the Euthyrisellidae and the Didymosellidae are described. All calcified walls are interior, and colony-wide (extrazooidal) basal coeloms are present in nearly all species. In the Family Euthyrisellidae, interzooidal visceral-to-hypostegal communication complements or even replaces the more usual, intrazooidal kind, which is that found in the Family Didymosellidae. In the Euthyrisellidae an extension of the hypostegal coelom on the basal side of the calcified frontal shield is present in most species. One new species, *Tropidozoum burrowsi*, is introduced. The Family Didymosellidae has a fossil record extending from the Middle Eocene to the Recent, and a wide Tertiary-to-Recent distribution. One new Recent species, *Didymosella pluma*, is introduced, and *Tubiporella boninensis* Borg is redefined. *Tubiporella levinseni* Borg is redescribed and assigned to the umbonuloid ascophoran genus *Reptadeonella*.

Introduction

The calcified and uncalcified body walls defining the member zooids of bryozoan colonies may conveniently be regarded as belonging to two kinds. The first is the exterior, limiting or boundary wall, which is primarily cuticular and which, if calcified, almost invariably has an outermost layer of cuticle throughout ontogeny. This kind of wall is actually or potentially capable of dividing the internal coelomic tissues of zooids from the environment. Zooids delimited by this kind of wall develop as uncalcified buds by expansion and extension of coelomic tissue through septulae in the calcified wall of an existing zooid. The boundary wall of cuticle and epidermis expands intussusceptively as growth proceeds. The earliest known, Late Jurassic cheilostomes had zooidal walls almost entirely of this kind (see Boardman & Cheetham, 1973), and large numbers of species now living have the same, or similar zooidal structure and budding pattern. Many lateral vertical walls of contiguous

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zooids in expanses of more integrated species are also exterior walls, even though they may appear to be 'inside' the colony. The second kind of wall is the interior wall, which may or may not possess any cuticular element, and which partitions existing coeloms and is not directly in contact with the environment. Zooids with interior walls are differentiated from a colony-wide expansion of coelom bounded by intussusceptively expanding cuticle and epidermis, by growth of a calcified lamina which, in earlier stages of ontogeny at least, is surrounded by coelom (see Boardman & Cheetham, 1973). Both kinds of wall have arisen several times in the long evolutionary history of the Bryozoa, and both kinds are usually to be found in any cheilostome colony. In some colonies, the distinction between the two kinds of wall is not clear cut. However, the astogenetic and ontogenetic sequences reflected by interior and exterior walls, and the intrazooidal and interzooidal communications associated with them, are important in the study of colony structure, of integration, and of systematic relationships through time.

Colonies with a high proportion of their calcified walls of the interior kind are well known among the 'free-living' anascan cheilostomes (Håkansson, 1973, Chimonides & Cook, 1981). Like these, several ascophoran Families, such as the Conescharellinidae, and genera such as *Sphaeropora*, as well as the Euthyrisellidae and Didymosellidae, have virtually no exterior calcified walls at all (Cook & Lagaaij, 1976, and Cook & Chimonides, 1981). The ascophoran forms show a much larger range of colony morphotypes than the anascan forms.

The species of Euthyrisellidae and Didymosellidae have cryptocystidean frontal shields (see Banta, 1970). These frontally placed parts of zooids in which the orifice is situated, are interior calcified walls which partition the visceral from the hypostegal coelom. The exterior frontal wall above the hypostegal coelom is completely cuticular, with underlying epidermal cells. In some species (e.g. *Pleurotoichus clathratus*) the frontal, cuticular wall is a continuous, colony-wide expanse, connected only intermittently with the vertical walls and the frontal shields. The lateral and distal vertical calcified walls are also interior walls, which partition a colony-wide coelom at the growing edge or tip of an expanse or branch. Basal calcified walls are also interior walls in the majority of species described here. These too, have communication with an extrazooidal basal coelom, which is protected from the environment by a cuticular and epidermal wall.

Intrazooidal, interzooidal and extrazooidal communication is an important feature in these colonies (Figs 1A, B) and its skeletal expression, in the form of septulae, and often in subsequent thickening of calcification, enables inferences to be made for fossil and Recent specimens in which the cuticular walls and coelomic tissues are no longer present.

Material and methods

The possibility of restoring recognizable structures, including muscles and viscera, in previously dried material, and the advantages of study of epoxy-resin mounted thin-sections of 'hard' and 'soft' tissues *in situ* have been demonstrated (Cook, 1975). Dried specimens were previously soaked in 10% trisodium phosphate solution for 48 hours, gently cleaned in detergent solution, and rinsed in water before staining. The accession of fixed, well-preserved material of *Pleurotoichus*, *Tropidozoum*, *Neoeuthyris* and *Didymosella* has enabled us to make sections which may be compared with those made from restored material. This comparison has tested the inferences drawn previously, and will allow further inferences to be made with greater confidence in the future.

Specimens for scanning electron microscopy were treated with sodium hypochlorite, rinsed and coated with gold-palladium. Specimens to be thin-sectioned were heavily stained in borax carmine or safranin, impregnated with epoxy-resin, cut and polished attached to 3″ × 1″ microscope slides.

Early attempts at embedding followed Nye *et al* (1972) and Sandberg (1971). Three resin types were available: Reichold Epotuf 37 128 with hardener 37 614, Shell Epon 812 and

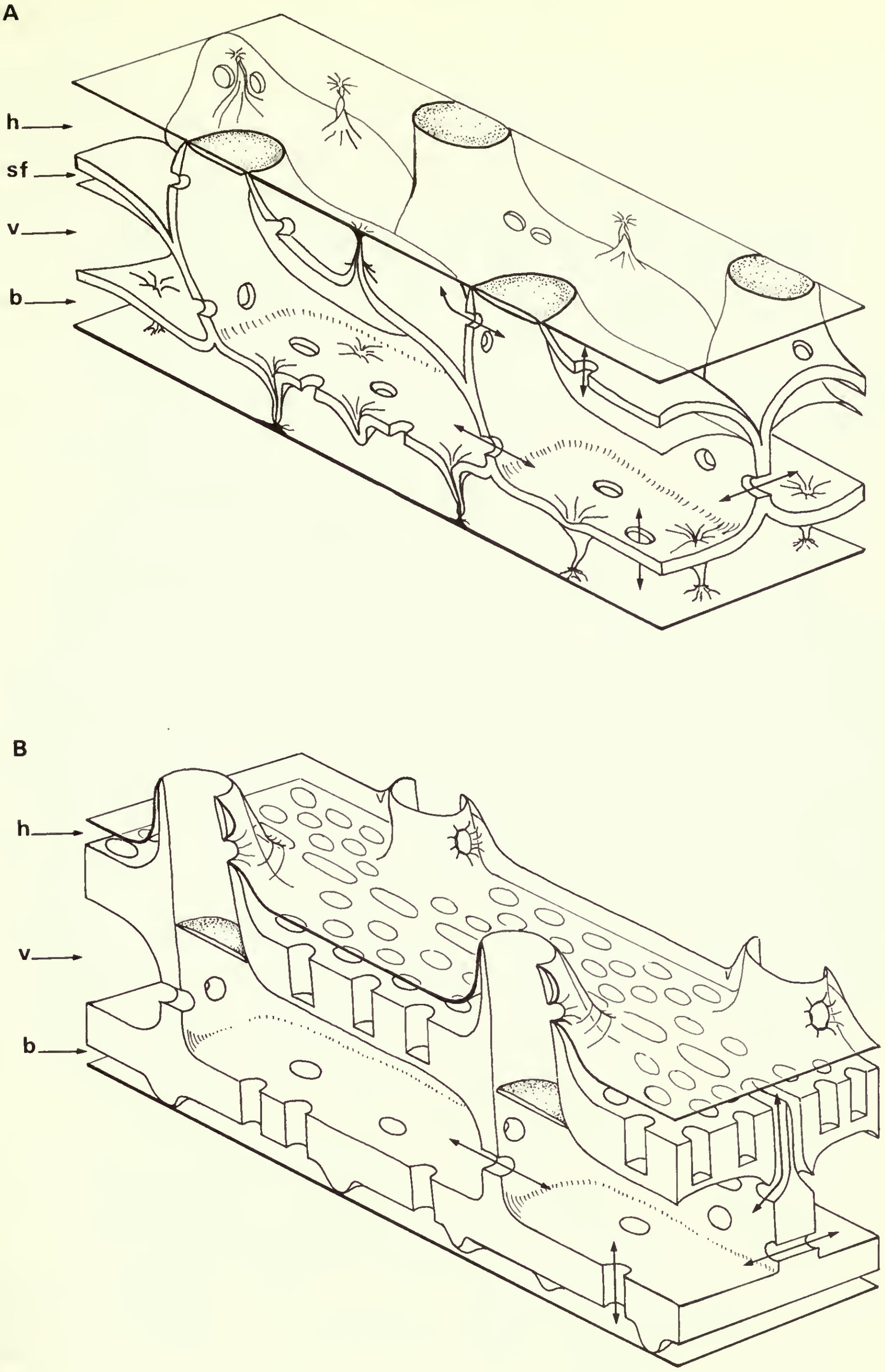


Fig. 1 Generalized diagrams to show residual communication after development of interior calcified walls in: (A) Euthyrisellidae; (B) Didymosellidae. Intercoelomic communications arrowed: *h* hypostegal coelom, *sf* subfrontal hypostegal coelom, *v* visceral coelom, *b* basal coelom.

Ciba Araldite CY212 with their complementary additives MNA, DDSA, BDMA, DMP 30 etc.

The Reichold resin, well tested by Nye *et al* (1972) was found to be difficult to use. The high viscosity of the components hindered obtaining the intended ratio of 4 parts resin to 1 part hardener and their subsequent mixing. The mix was found to be sensitive to heat and U.V. light (e.g. sunlight) and there was a tendency for thermal runaway to occur. This reaction was more readily provoked if the mix contained slightly excess hardener, even though the plug size was only 30 cm^3 and curing was initiated at room temperature, 20°C. It was found that surface temperatures in excess of 80°C were reached, coupled with emission of phenol-smelling fumes, bubbling and volumetric expansion. When curing could be controlled by refrigeration a volumetric contraction, estimated as 8% total, was noted. No significant change in behaviour was noted with prolonged storage of the components at 5–10°C. The recommended life of hardener 37 614 is given as 6–12 months in a tightly closed container at room temperature or less. Denaturing is characterized by progressive discolouration to a dark brown colour. Epon 812 was used as described by Sandberg (1971) using only MNA as hardener. DMP 30 and BDMA (Glauert, 1965, 1974) were used as accelerators in parallel series. Araldite CY212 was used in the same way. The preferred ratios of the components were: resin 54%, hardener 44% and accelerator 2%. Both resins were found to have tolerant curing temperatures of 50–80°C. Epon 812, with its low viscosity and production of relatively clear and hard plugs promised to be the ideal medium. It was found, however, that as lapping of thin-sections progressed, small, granular particles of resin (and sometimes of specimen) would break away leaving score marks on the polished surface. This was more noticeable as the thickness of the preparation reached 40 μ or less. It was almost impossible to produce an intact section below 20 μ. Freeman & Spurlock (1962), in electron microscopical studies, reported Epon 812 as being inherently granular. This suggests that thin-section disintegration may be a larger scale manifestation of the same characteristic. The disintegration problem was more pronounced at the lower curing temperatures. In addition, it was found that the resin in sections became 'milky' in aqueous solutions (even without the aquon component), or in the lapping lubricant used, Engis Hyprez type W. The resin would also accept stains which were difficult to remove. Further, as the section was thinned, it would distort and lift from the slide. These effects were noted regardless of resin and additive batch and of precautions to ensure uniform mixing of components and cleanliness of the glass slides. A noticeable volumetric contraction (of about 6–7%) was again found, regardless of recipe and of curing procedure.

Araldite CY212, in spite of its high viscosity, was found to be the most suitable resin. Its total curing contraction was estimated as 1–2%, regardless of recipe. Stability during lapping was high, and it was possible to obtain sections in the order of 3 μ thickness. One disadvantage was that xylene affected the cured resin and coverslides mounted with Canada balsam were therefore avoided. Where required, coverslides were mounted using more epoxy-resin.

In all cases propylene oxide was used as the antemedium. Final embedding was vacuum assisted after first soaking the specimens in an equal mixture of propylene oxide and accelerated resin mix. One well known advantage of the use of propylene oxide is that any residual quantities trapped in the specimen should polymerize with the resin.

In all resins used, behaviour appeared equally divided between pre- and post-gel contraction. Reichold Chemicals Inc. (*pers. comm.* 16.2.1977) suggested that a more typical contraction behaviour of their resin would be approximately 5% total, distributed as 3% pre-gel and 2% post-gel phase. Potter (1970 : 171) identified post-gel shrinkage as the phase at which stresses may be introduced which can lead to damage, although his account relates to electrical component encapsulation and is without reference to scale. It was indicated that post-gel contraction for epoxy resins is normally in the region of 2–3% and that contraction overall is affected primarily by the accelerator used.

In making thin-sections the effects of resin contraction were most apparent when attaching preparations to microscope slides, when bowing of the glass, and in many cases, even breaking was noted. The amount of resin was therefore kept to a minimum, and Araldite resin obviously showed to advantage.

Within the specimen itself, shrinkage should have little effect providing that complete penetration by the resin has been achieved. Although penetration may appear to be complete, it has been found, during cutting and polishing stages, that calcified walls may drop out of the section completely, as opposed to partial fracturing and partial loss. This indicates a lack of specimen support.

If a final surface stain was applied, there was a tendency for the stain to delineate the boundary of the calcification, although it should be borne in mind that the micro-relief produced by lapping may have been a contributory factor. In sections of 10 μ thickness or more, the stain sometimes soaked into the boundary irregularly. Support failure and staining characteristics suggest an unpredictable penetration of the resin into the calcification, together with a degree of incomplete adhesion which may be exacerbated by resin shrinkage. The evidence is at present considered to be inconclusive, especially as the effects were observed most often when using the structurally unsatisfactory Epon 812 resin. For these reasons staining before embedding was preferred.

Measurements and abbreviations used

The value of comparative measurements among, for example fossil and Recent colonies of the same or different species, varies considerably among bryozoans, both with the structures measured and with the species groups being investigated. For example, some species retain recognizable traces in frontal view, of structures such as the tops of vertical walls, throughout ontogeny and in spite of wear. In such species comparisons of zooidal length and width among colonies are easily made and are significant. Primary calcified orifices with distinct boundaries are also capable of yielding reasonably accurate measurements. In the species considered here, one family, the Euthyrisellidae, which has no fossil record, retains throughout ontogeny recognizable features which allow morphometric analysis. The Didymosellidae, on the other hand, includes species in which continuous ontogenetic changes throughout colony life obscure zooidal boundaries and primary orifices, which in themselves are not easily definable. Fossil (and some Recent) specimens, which have been damaged or are worn, are therefore not strictly comparable with well preserved colonies. Other micro-environmental effects, such as those influencing the length of peristomes, may sometimes be recognized, but are difficult to quantify.

Abbreviations

Measurements in millimetres

Length of autozooid	Lz	Width of autozooid	lz
Length of brooding zooid	Lbz	Width of brooding zooid	lbz
Length of primary orifice	Lo	Width of primary orifice	lo
Length of brooding z. orifice	Lbo	Width of brooding z. orifice	lbo
Length of rostrum	Lr	Width secondary orifice	l2o
Length of mandible	Lm		

BMNH	British Museum (Natural History)	MM	Manchester Museum
NMV	National Museum of Victoria	AM	Australian Museum, Sydney.
ZMA	Zoological Museum, Amsterdam	SAM	South African Museum, Cape Town.

Key to species described

1 Raised peristomes absent, opercula well-developed, often with two layers and with complex sclerites. Frontal pores and septulae absent or rare; large frontal foramina present or absent. Avicularia and ovicells usually absent. Secondary calcification slight. Brooding zooids strongly dimorphic . . . . **EUTHYRISELLIDAE** 2

– Raised peristomes present, opercula simple, not usually visible. Frontal pores and septulae numerous. Avicularia and ovicells present. Secondary calcification extensive. Dimorphic zooids not obvious . . . . **DIDYMOSELLIDAE** 6

2 Colonies encrusting, avicularia and ovicells present, basal coelom absent ***Neoeuthyris woosteri*** p. 67

– Colonies erect. Avicularia and ovicells absent, basal coeloms present 3

3 Colonies flustriform, unilaminar, with lateral and basal coeloms 4

– Colonies cellariiform, with kenozooidal nodes. Internodes with zooids in curved, laterally contiguous series. Basal coelom forming a central column . . . ***Tropidozoum*** 5

4 Frontal shield complete, smooth. Lateral coeloms with series of calcified plates . . . . ***Euthyrisella obtecta*** p. 60

– Frontal shield with calcified bars and large, slit-like foramina. Lateral coeloms without series of calcified plates . . . . ***Pleurotoichus clathratus*** p. 63

5 Autozooidal orifices not sinuate, frontal shield with large foramina ***Tropidozoum cellariiforme*** p. 64

– Autozooidal orifices with a deep, triangular sinus, frontal shield with small foramina . . . . ***T. burrowsi*** sp.nov. p. 65

6 Peristomes with large, paired proximal foramina, spiramen absent . ***Didymosella*** 7

– Peristomes with one, or no foramen, spiramen present . . . . . ***Tubiporella*** 13

7 Colonies erect, ligulate, unilaminar. Zooids in 2–5 transverse rows. Basal pores present 8

– Colonies encrusting, semi-encrusting or repent, or bilaminar or cylindrical . . . 9

8 Branches flat, 4–5 zooids wide, basal pores numerous ***Didymosella porosa*** p. 72

– Branches laterally curved towards the basal side, 2–3 zooids wide, basal pores rare ***D. clypeata*** p. 72

9 Colonies bilaminar or cylindrical ***D. larvalis***-complex (fossil populations) p. 73

– Colonies unilaminar or semi-encrusting, with large basal foramina, or basal pores and/or calcified processes 10

10 Colonies encrusting or semi-encrusting. No coelom basally, but zooid walls uncalcified or with a large, central foramen. Peristomes deficient distally, raised proximally ***D. larvalis***–complex (Recent populations) p. 73

– Colonies repent, with basal pores and/or long calcified processes. Peristomes tubular . 11

11 Zooids large $Lz > 0{\cdot}70$ mm), avicularian rostra with an open channel terminally 12

– Zooids smaller ($Lz < 0{\cdot}70$ mm), avicularian rostra very small and acute ***parviporosa*** p. 75

12 Zooids with more than 25 frontal pores. Basal surface with pores (fossil) ***D. crassa*** p. 71

– Zooids with less than 25 frontal pores. Basal surface with long, calcified processes. Avicularian mandible expanded laterally (Recent) . ***D. pluma*** sp. nov. p. 76

13 Colonies forming broad, repent expansions. Peristomes with a single foramen early in ontogeny. Avicularia with acute, hooked mandibles ***Tubiporella magnirostris*** p. 77

– Colonies ligulate, 4–7 zooids wide, repent. Peristomes entire, very long and tubular. Avicularia elongated, with laterally expanded mandibles . ***T. boninensis*** p. 79

Systematic Section

EUTHYRISELLIDAE Bassler

Euthyrisellidae Bassler, 1953 : G226.

TYPE GENUS. *Euthyrisella* Bassler, 1936.

DESCRIPTION. Interior walled cryptocystidean ascophorans, usually with extrazooidal, cuticle-bounded basal coeloms. Colonies encrusting algae, or erect, flexible, rooted. Zooids

Table 1 Average measurement (mm) of zooids of Euthyrisellidae.

	Lz	lz	Lbz	lbz	Lo	lo	Lbo	lbo
E. obtecta	0·55	0·35	0·73	0·52	0·15	0·19	0·20	0·27
P. clathratus	0·55	0·37	0·60	0·51	0·24	0·24	0·24	0·31
T. cellariiforme	0·65	0·34	0·73	0·38	0·21	0·18	0·24	0·19
T. burrowsi	0·67	0·36	0·67	0·50	0·21	0·15	0·15	0·20
N. woosteri	0·90	0·41	1·60	0·50	0·23	0·17	0·26	0·31

with relatively little secondary calcification frontally, frontal septulae restricted or absent. Hypostegal coeloms extensive, often extending basally to the calcified frontal shield, and communicating interzooidally with visceral coeloms of zooids of the previous astogenetic generation. Externally obvious brooding structures and avicularia usually, but not exclusively absent. Orifices of brooding zooids enlarged, dimorphic.

REMARKS. The family was introduced by Bassler (1953) for the genera *Euthyrisella*, *Pleurotoichus*, *Neoeuthyris* and *Urceolipora*. The relationships among these genera have been discussed by Levinsen (1909), Harmer (1957) and Hastings (1964). *Urceolipora* shows many characteristics in common with *Euthyrisella* and *Neoeuthyris* on the one hand, and with the genera *Calwellia* and *Icthyaria* on the other. These generic groups, together with others which have some similarities in their colony organization, such as *Onchoporella* and *Euthyroides* all require detailed analysis, but are beyond the scope of this paper. *Urceolipora* is therefore excluded here, but the genus *Tropidozoum* is included in the family.

ONTOGENY OF ZOOID WALLS. In all species, the primary ontogenetic changes in calcification of the zooid walls and formation of the orifice, operculum and ascus, appear to be very rapid, as few intermediate stages between undifferentiated buds and complete zooids are present. In addition, growth appears to proceed in distinct episodes, alternating with periods of astogenetic quiescence, as many colonies show little evidence of any zones of developing zooids at the growing edges or tips, and some colonies show distinct 'growth lines' (see below).

Where present, the growing zones consist of an undifferentiated area of coelomic tissue bounded by thin cuticle. The calcification of interior walls proceeds distally, and the lateral walls become intermittently attached to the frontal cuticle. At the same time the opercular cuticle becomes thickened and differentiated. Where there is a basal coelom, the calcified lateral walls converge, forming a basal zooid wall which may be linear, or merely a curved continuation of the lateral walls. Contact with the cuticular, basal colony-wide wall occurs later in ontogeny in some species. The development of the lophophore and viscera is complete 2–3 zooid generations from the growing zone, just in advance of the final stages of ascus development (see also Harmer, 1902).

In *Tropidozoum*, particularly *T. burrowsi* (see p. 65, there is some subsequent thickening of the calcification of the frontal shield and basal walls. In *Euthyrisella*, *Pleurotoichus* and *Neoeuthyris*, thickening is confined to the development of processes attaching the cuticle to the frontal shields, or to the development of calcification within the lateral extrazooidal coeloms, when present.

Coelomic systems and communication

The intercommunication among the hypostegal, visceral and extrazooidal coeloms is considerable, and reflects the varying extent and patterning of these coeloms throughout the colony (Fig. 1A). The virtual isolation of the hypostegal coelom, particularly in *Tropidozoum*, is a direct result of the rarity of the frontal septulae (areolae) usually found in cryptocystidean ascophorans, and is accompanied in most species by an extension of this coelom beneath the calcified frontal shield (see also Cook, 1975). Transfer of nutrients in coelomic fluids is inferred by the presence of communication pores in the distal-terminal or distal-lateral calcified walls, which connect the visceral coelom of one zooid with the hypostegal coelom of the next successive, distal zooid. This system, too, is unusual in cheilostomes, although it probably occurs in the genera *Urceolipora*, *Calwellia* and *Onchoporella* as well (see above). The basal and lateral extrazooidal coeloms are extensive in all the erect genera, but absent in *Neoeuthyris*, which is encrusting. Where present, they are inferred to function connectively and, as their cuticular walls thicken with ontogeny, to become involved in the anchoring and support of the colony.

Opercula

The opercula are large and double layered, with strengthening sclerites in most species. The morphology of the complex opercula of *Euthyrisella* and *Pleurotoichus* has been fully described by Harmer (1902). Those of *Tropidozoum* and *Neoeuthyris* are simpler in construction, but also have strong sclerite systems.

Brooding zooids

All species show dimorphism of brooding zooids, the larger dimorphs having enlarged orifices and, in the erect species, swollen basal walls. Embryos have now been observed in all species and without exception, are associated with the larger dimorphs. They are not readily seen except by transmitted light (cf. Harmer, 1902), but when present, usually fill the central and proximal parts of the cystid and are presumably contained in ovisacs.

The ovicells of *Neoeuthyris* differ considerably in appearance from the brooding zooids of the other genera. However, the brooding cavity may be regarded as a displacement of the swollen basal cavity in a distal and frontal direction. This is correlated with the encrusting mode of life, which does not allow basally directed expansion.

EUTHYRISELLA Bassler

Euthyrisella Bassler, 1936 : 161 (for *Euthyris* Hincks *preocc.*)

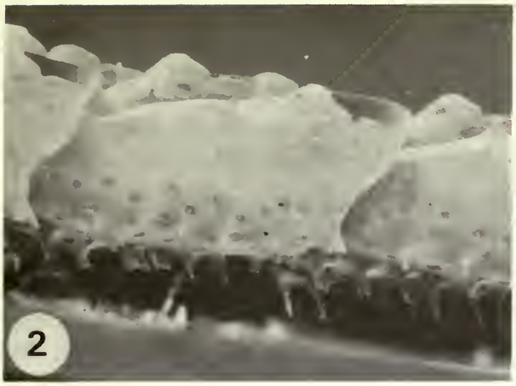
TYPE SPECIES. *Euthyris obtecta* Hincks, 1882.

DESCRIPTION. Colony flustriform, branching, multiserial and unilaminar, with basal and marginal extrazooidal coeloms bounded by cuticular walls, which become thickened to form anchoring, rooting structures, with internal calcified plates late in ontogeny. Zooids with depressed, curved, thinly calcified frontal shields, with few pores. Lateral walls converge basally and are attached to the basal cuticular wall by intermittent calcified processes. Dimorphic brooding zooids inflated basally, with enlarged orifices and opercula.

Euthyrisella obtecta (Hincks)

Euthyris obtecta Hincks, 1882 : 164, pl. 7, fig. 3, 1893 : 177. Harmer, 1902 : 277, pl. 16, figs. 32–37. Levinsen, 1909 : 272, pl. 15, figs 2a–f. Canu & Bassler, 1929 : 464, Figs 199 A–M.

Figs 2–7 Scanning electron micrographs of Euthyrisellidae: (2) *Euthyrisella obtecta* (Hincks) BMNH 1890.3.24.22, Torres Straits, lateral view of zooids showing lateral and oral septulae and basal processes ×65; (3) *E. obtecta*, zooids viewed from distal end, showing distal septulae (arrowed) and frontal processes ×120; (4) *Tropidozoum cellariiforme* Harmer BMNH 1964.3.10.1, Celebes, frontal view of primary zooids of internode, showing calcified tube at distal end of nodal kenozooid ×72; (5) *T. burrowsi* sp. nov. BMNH 1975.1.4.1, Madagascar, basal view of proximal part of internode, showing autozooids and basal coelomic column, with basal septulae and bars of calcification ×30; (6) *T. burrowsi*, frontal view of autozooids and brooding zooid ×53; (7) *Neoeuthyris woosteri* (MacGillivray) BMNH 1979.2.1.1, Western Australia, frontal view of autozooids and avicularia ×30.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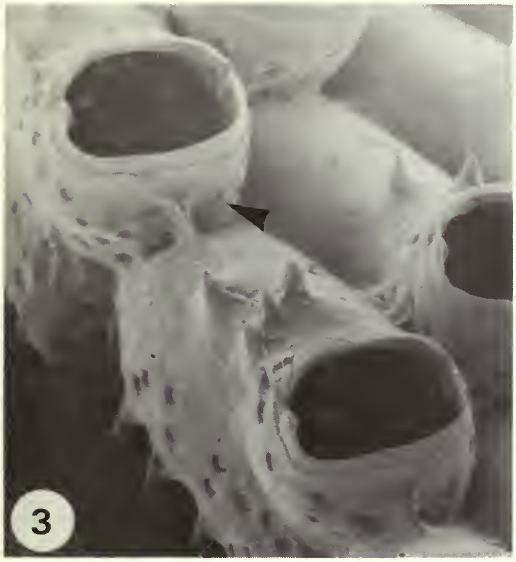
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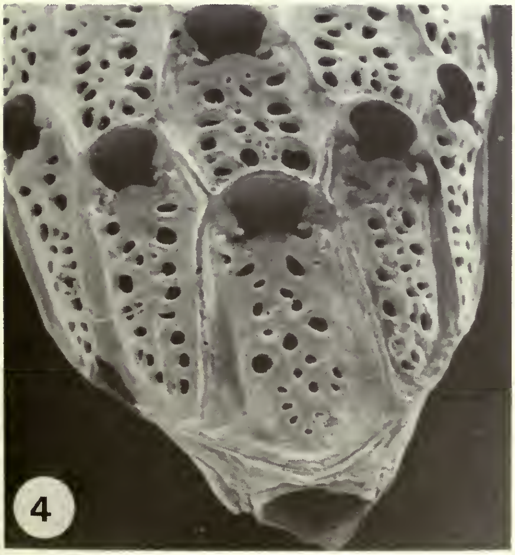
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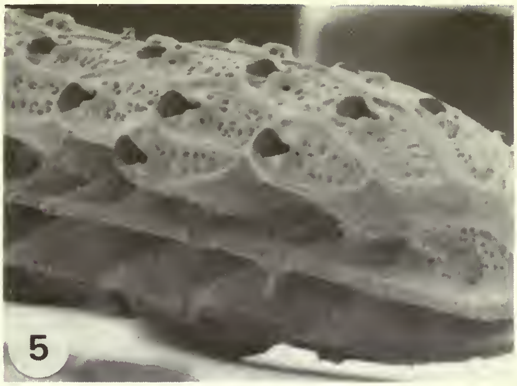
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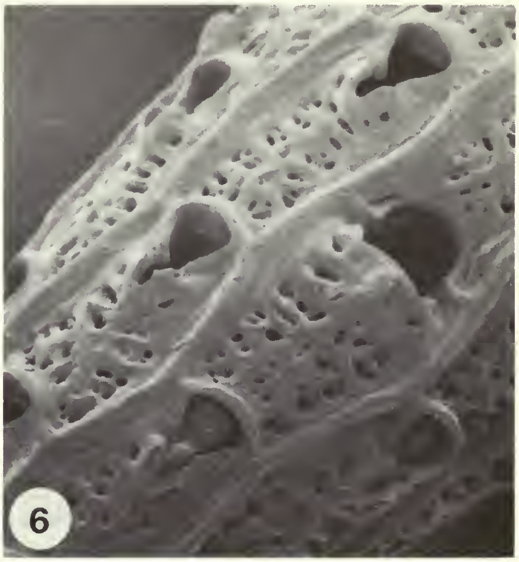
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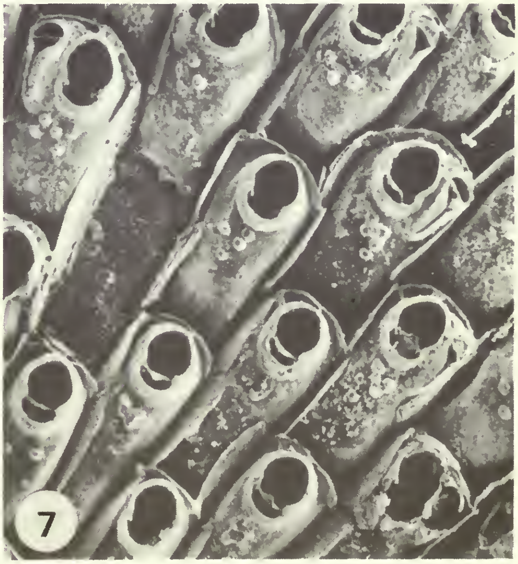
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SPECIMENS EXAMINED. BMNH. North Australia, 1897.5.1.445 (possibly type material); Broughton Id., New South Wales, 1883.11.29.3; Port Denison, East Queensland, 1883.11.29.43; Murray Id., Torres Straits, 1890.3.24.22, 16–36 metres; 1890.7.23.38, 17–36 metres; 1916.8.23.115, 9–36 metres; Baleine Bank, Northwest Australia, 1892.1.28.34A, 17–22 metres; Holothuria Bank, Northwest Australia, 1892.1.28.61A, 22 metres; Long Reef, 5 miles North of Sydney, New South Wales, 1975.1.2.3, 101 metres.

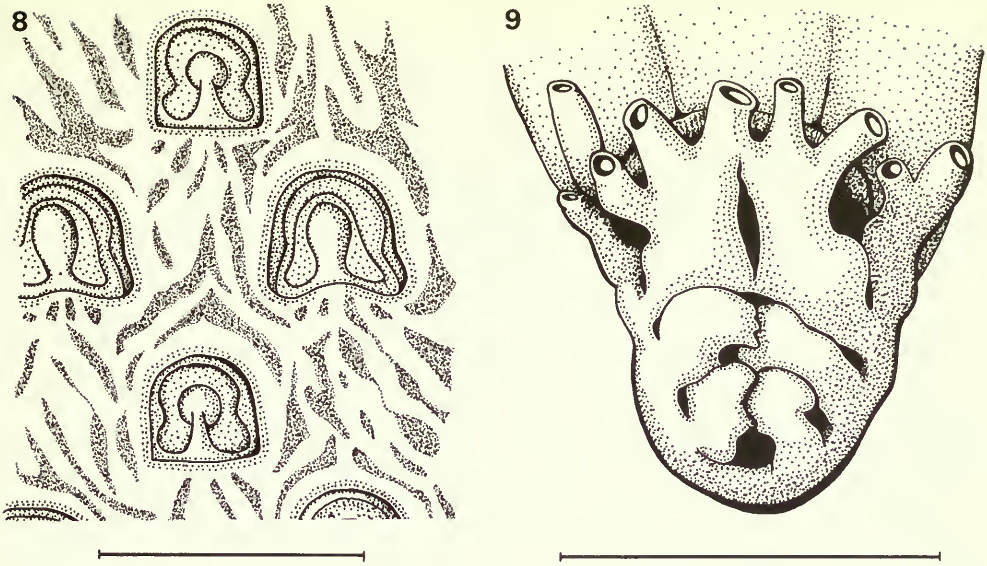
DESCRIPTION (Figs 2, 3, 33, 35). *Euthyrisella* with zooids intercommunicating by 6–8 lateral septulae (8–10 in brooding zooids) and 5–6 distal septulae. Zooids with 12–20 basal septulae (45–50 in brooding zooids) and 2–8 septulae distal to the orifice, which communicate with the hypostegal coelom of the next distal zooid. Frontal shield thinly calcified, with 2–5 pores proximal to the orifice (10–15 in brooding zooids), some of which are septulae communicating with the part of the hypostegal coelom basal to the frontal shield. Orifices with small lateral condyles. Dimorphic (brooding) zooids about twice the size of the autozooids.

REMARKS. The hypostegal coelom beneath the frontal shield is not nearly as extensive as in *Pleurotoichus* and *Tropidozoum* (see below), but forms a small expansion proximally to the orifice (Fig. 35). The dimorphic brooding zooids occur in a proportion of approximately 1 : 20 autozooids. Large embryos are present in one colony from Torres Straits (1890.7.23.38).

The colonies are profusely branched and reach a height of 150 mm. The branches are 2–3 mm wide and are usually formed by simple bifurcation, but some, astogenetically late, lateral branches occur. Before a bifurcation the width increases to 4 mm, and the number of zooids in a transverse series from 3–4 to 5–6. There is a tendency for one branch of a bifurcation to include more zooids than its pair. At irregular intervals there is an increase in the width which does not result in a bifurcation, but a sudden decrease in zooid numbers between successive generations. This seems to be associated with a period of cessation of growth, as the basal cuticle is much thicker on the proximal side of the interruption.

The early astogeny has been inferred from one colony (1883.11.29.3). A single, erect kenozooid is followed by a distal zooid which itself buds one distal and paired distal-lateral zooids. Thereafter, increase in zooid rows originates from bifurcations of series distal to marginal zooids. At the base of fronds zooids have the series: Lz 0·50, 0·50, 0·67, 0·50, 0·53, 0·58, 0·60 mm. The only other astogenetic changes are confined to brooding zooids which do not appear until the branch is 100 mm in length (300 zooid generations). Brooding zooids are central and often paired in the same transverse series.

The extrazooidal marginal coelomic systems are extensive and resemble those formed by lateral kenozooids in several anascan, flustriform genera and the ascophoran species *Euthyroides episcopalis* and *Onchoporella buskii.* The changes during colony growth may be regarded as ontogenetic, in that they occur within the bounding walls of an existing structure. The primary changes are found 40 zooid generations back from the growing tip. The lateral cuticle expands intussusceptively and thickens considerably. About 150 zooid generations back, calcareous spicules derived from the lateral walls of the marginal zooids expand and form a series of plates within the lateral coeloms. Subsequent series of plates, alternating with cuticle, are formed at the base of the colony, and the investing cuticular wall continues to expand and thicken (see Harmer, 1902). At the earliest astogenetic level there are 9–12 series of thickened plates on each side of the branch. The growth of anchoring rootlets is also an ontogenetic rather than an astogenetic change. The marginal elements extend basally and divide into rhizoids which penetrate the substratum, incorporating particles of sediment within a meshwork. Some calcification occurs so that the rhizoids are not only flexible but adherent. It is possible that further extensions are astogenetic and consist of kenozooids budded from the extrazooidal coeloms. It is interesting that an almost identical series of calcareous plates occurs in the kenozooidal, lateral rooting systems of *O. buskii.* The rooting system of the colony (1883.11.29.3) has incorporated the substratum of shell fragments, sand grains, foraminiferans and dead bryozoans. Although these last are worn, and may have been transported, it is interesting that they comprise



Figs 8 and 9 (8) *Pleurotoichus clathratus* (Harmer) BMNH 1976.1.2.1, Heron Island, sketch of frontal surface of autozooids and brooding zooids, showing opercula and irregular bars of calcification of frontal shield beneath the cuticular frontal wall; (9) *Didymosella larvalis* (MacGillivray) BMNH 1890.4.17.1–10pt., Spencer Gulf, sketch of ancestrula. Scale bars = 0·50 mm.

rooted 'sand fauna' species (see Cook, 1965, 1966, 1979*b*). They include colonies of *Conescharellina* sp., the internodes of jointed species of cyclostomes and of the cheilostome anascan, *Exostesia didomatia* (see Brown, 1948 : 111). Other epizoic forms include a ramifying hydroid and numerous egg sacs of some unknown animal.

PLEUROTOICHUS Levinsen

Pleurotoichus Levinsen, 1909 : 270.

Type species. *Euthyris clathrata* Harmer, 1902.

Description. Colony flustriform, branching, multiserial, unilaminar, with marginal and basal extrazooidal coeloms. Zooids with flat, depressed frontal calcified shields consisting of irregular bars and foramina, each bar surrounded by cuticle. Lateral walls curved and converging, basal walls linear, reaching the extrazooidal basal wall in discontinuous series. Dimorphic zooids slightly larger than autozooids, with larger opercula, inflated basally. Lateral coeloms slightly calcified late in ontogeny.

Pleurotoichus clathratus (Harmer)

Euthyris clathrata Harmer, 1902 : 266, pl. 16, figs 18–31.
Pleurotoichus clathratus : Levinsen, 1909 : 270. Canu & Bassler, 1929 : 464, Figs 200 A–N.

Specimens examined. BMNH. Australia, 1899.7.1.2606; Port Jackson, New South Wales, 1903.5.1.2, sublittoral; Swan River, South Australia, 1935.10.18.1; Middle Harbour, Port Jackson, 1975.8.1.7; Watsons Bay, 1975.8.1.8.9, under rock ledges, low tide; Heron Id., Queensland, 1976.1.2.1.

Description (Figs 8, 34). *Pleurotoichus* with zooids communicating by 7–9 lateral and 7–10 distal septulae. Zooids with 12–15 basal septulae, and 3–5 distal to the orifice, communicating with the hypostegal coelom of the next distal zooid. The frontal shield is formed by irregular cuticle-covered bars, which anastomose, leaving large slit-like foramina. The hypostegal coelom is extensive both above and below the shield. The dimorphic brooding zooids are only slightly larger than the autozooids; they are inflated basally, and occur in larger numbers than in *E. obtecta*, in a proportion of 1 : 5 autozooids.

REMARKS. The presence of cuticle surrounding the bars of calcification of the frontal shield, and the layers of cuticle on either side of the lateral and distal calcified walls, together with the general delicacy of the interior structures, makes it almost impossible to prepare calcified skeletons of *P. clathratus* for scanning electron microscopy. Investigation of specimens has therefore been almost entirely confined to examination of thin-sections. The hypostegal coelom, both frontal and basal to the calcified shield is very extensive. The convergent lateral walls reach the basal cuticular extrazooidal wall in one short, linear insertion. The calcified processes are cuticular terminally at the point of contact. Zooids are thus almost suspended from the circum-orificial region in a bag of tough, flexible cuticle. This flexibility is probably correlated with the turbulence of the very shallow waters in which the species lives. The growth form is analogous to that of *Chartella papyracea* (see Ryland & Hayward, 1977 : 80), which also inhabits rocky ledges in the sublittoral region.

Colonies may reach a height of 185 mm (Harmer, 1902 : 268). The specimens examined have a maximum height of 50 mm, and have very few bifurcations. A few lateral sub-branches occur late in astogeny. The earliest stages are missing, but may be inferred from a colony from Port Jackson (1975.8.1.7), which has 4 zooids in a transverse row at its base. Extrapolating from this, the early astogeny is probably similar to that of *E. obtecta*, and the zooids show a similar series of increase in size. Interruptions of growth, involving a sudden decrease in the number of zooids in transverse series from 6–7 to 3–4, occur frequently, between 6 and 10 zooid generations apart.

Dimorphic zooids are frequent (Fig. 2), and are first found 25 generations from the base of the colony. They are placed in the central zooid series, and large embryos are present in the colony from Heron Island (1976.1.2.1.).

The marginal coeloms become inflated with ontogeny, and the cuticular walls become thickened. Small calcified processes develop from the lateral walls of adjacent zooid series, but calcified plates do not occur.

The colony from Heron Island has a large number of epizoic forms, particularly colonies of hydroids. On the basal cuticle there are small colonies of jointed cyclostome bryozoans and of *Cellaria* sp. The lower part of the colony is completely invested by a colonial ascidian.

TROPIDOZOUM Harmer

Tropidozoum Harmer, 1957 : 1106. Cook, 1975.

TYPE SPECIES. *T. cellariiforme* Harmer, 1957.

DESCRIPTION. Colony cellariiform, internodes connected by complex nodes of partially calcified kenozooids and investing extrazooidal basal coelom. Basal coelomic channel confluent among internodes. Central zooids of internodes with extended basal calcification forming a keel. Zooids with depressed frontal shields, with large foramina. Hypostegal coelom extensive, frontal septulae absent. Brooding zooids large, inflated basally, with dimorphic orifices.

Tropidozoum cellariiforme Harmer

Tropidozoum cellariiforme Harmer, 1957 : 1106, pl. 67, figs 15–17, 20. Cook, 1975 : 162, pl. 2, pl. 3, Figs 2A, 3 (explanation of plates 1 and 3 transposed). Cook, 1979a : 200, pl. 1, fig. 1.

SPECIMENS EXAMINED. BMNH. Siboga Stn 144, South of Halmaheira, Djilolo, East Celebes, 0–45 metres, coral and lithothamnion bottom, 1964.3.10.1 and 1979.1.4.1.

ZMA, as above, TYPE and other material.

DESCRIPTION (Figs 4, 11, 30). *Tropidozoum* with internodes 8 mm long and 1·6 mm wide, comprising 70 zooids. Longest, usually the central series, of 12 zooids; widest, usually the penultimate transverse series, of 6 zooids. Zooids occupying an arc of 240° in section. The proximal zooid of each internode is wider (Lz 0·37 mm), and the ultimate zooids shorter and narrower (Lz 0·50, lz 0·30 mm), than other zooids. Orifice rounded distally with large complex condyles delimiting a proximal part which is straight or curved distally. Frontal shield with up to 30 large, irregular foramina. Hypostegal coelom extending beneath the frontal shield. Communication between the visceral coelom of one zooid and the hypostegal coelom of the next distal zooid inferred to be through a pair of minute pores passing through the distal-lateral calcification of the orifice (Fig. 30). Communication with the basal coelom through numerous pores in the confluent lateral and basal walls. Brooding zooids dimorphic, large, inflated basally, placed in the central zooid series, occurring in the proportion of 1 : 10 autozoids. Brooding zooid orifices larger, but similar to those of autozoids.

REMARKS. The earliest astogenetic stages are missing from the colonies examined, but it is inferred that they are similar to those of *T. burrowsi* (see below). The cuticle of the basal coelom becomes increasingly thickened and inflated with ontogeny, and eventually forms a supportive and rooting structure.

The septulae connecting the visceral and hypostegal coeloms of sequential zooids are very small, and apparently pass through the thick calcification distal and lateral to the orifice. The tubular communication traces a curved path, at an angle to the longitudinal axes of the zooids, and is impossible to expose in its entirety in either longitudinal-lateral or in tangential thin-section. The pattern of other zooidal and extrazooidal communications has been described by Cook (1975).

A few, small embryos have been seen in the brooding zooids. The distal part of the orifice of these zooids appears to be formed by the proximal calcification of the next distal zooid (see Fig. 30).

Epizoic forms include other erect, jointed bryozoans such as *Cellaria* sp., small colonies of a *Bowerbankia*-like ctenostome, encrusting colonies of *Robertsonidra argentea* (Hincks), and foraminiferans belonging to the informal '*Homotrema*' group.

Tropidozoum burrowsi sp. nov.

Tropidozoum sp. Cook, 1975 : 165, pl. 1, figs A–C, Fig. 2B (explanation of Plates 1 and 3 transposed). Hayward & Cook (in press).

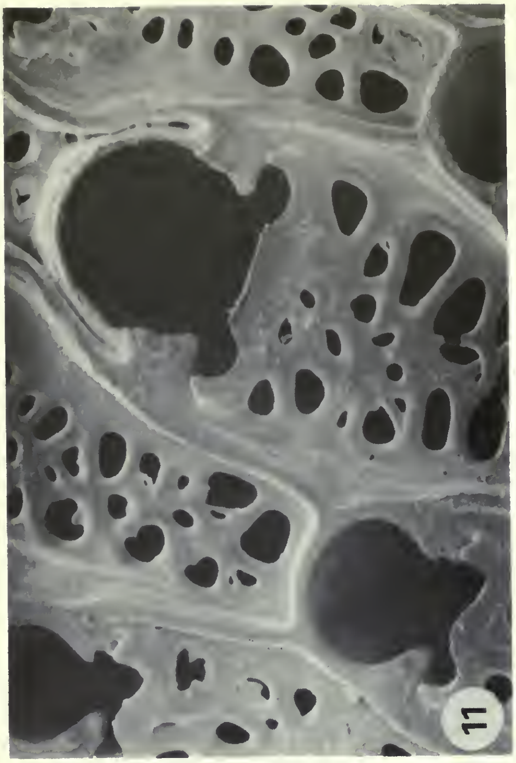
SPECIMENS EXAMINED. BMNH. HOLOTYPE, Tuléar, TU 24, Madagascar, extérior Grande Vasque, 23.9.69, 15 metres, 1975.1.4.2. Paratypes, Tuléar, Pichon D25, 1975.1.4.1; other material: South of Durban, Umtwalume River mouth North by West 7 miles, 12271, shell fragment bottom, 90 metres, 1949.11.10.184, and 12272, 1949.11.10.250, transported, dead internodes.

SAM. '*Meiring Naude*', Southeast Africa, Stn 131, 780 metres, Stn 151, 900 metres, transported, dead internodes.

ETYMOLOGY. Named after Mr H. W. Burrows, whose manuscript notes and drawings on the Gilchrist Collection from South Africa are stored at the BMNH.

DESCRIPTION (Figs 5, 6, 10). *Tropidozoum* with internodes 7 mm long and 1·1 mm wide, comprising 70 zooids. Longest longitudinal series of 16 zooids; widest, penultimate transverse series of 6 zooids. Zooids occupying an arc of 300° in section. Proximal and ultimate zooids wider than other zooids. Central basal keel thickened by base of calcification during ontogeny. Orifices rounded distally, with large condyles delimiting a deep, triangular sinus. Frontal shield with 30 small, irregular foramina, occluded during ontogeny. Dimorphic brooding zooids inflated basally, larger than autozooids, with wide, non-sinuate orifices.

REMARKS. The early stages in astogeny of erect branches arise from a confused mass of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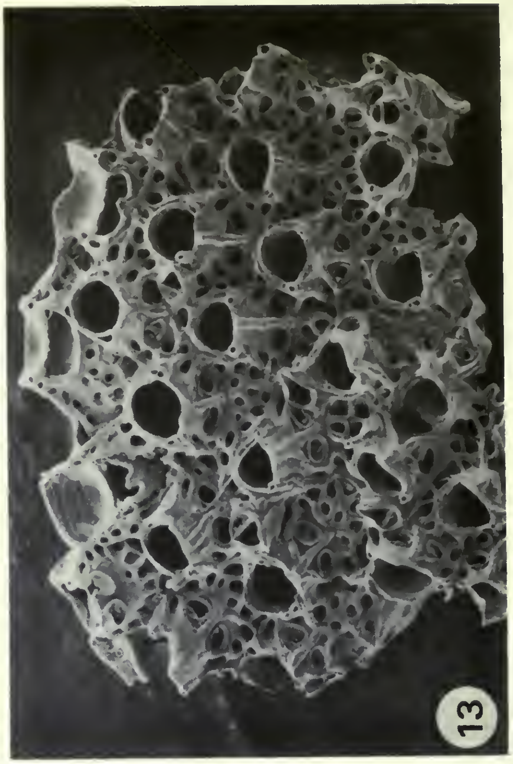
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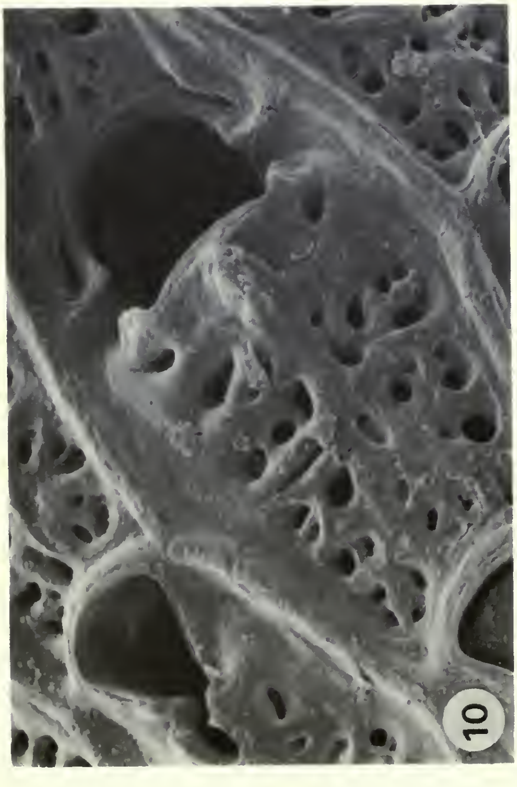
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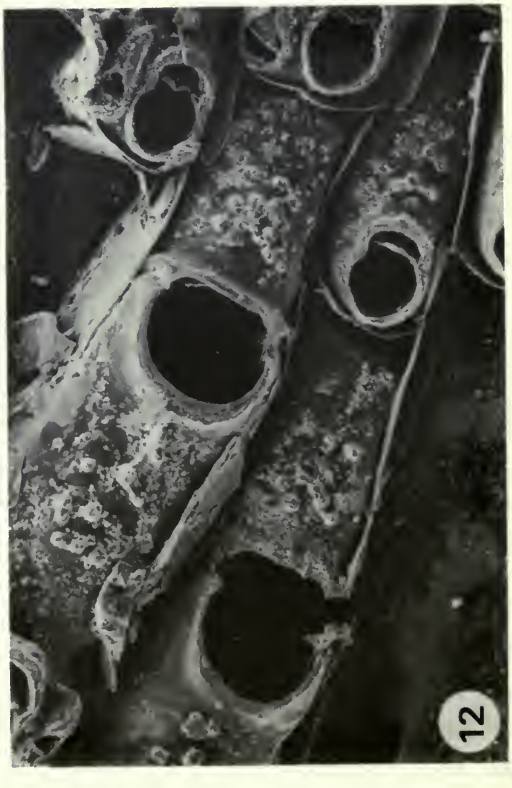
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rooting kenozooids, and it is not known if these represent one, or a large number of colonies. Some kenozooids are rootlets, others are shorter, and from these small erect internodes originate. The maximum number of internodes in an erect branch is 15, reaching a height of 130 mm. The primary internodes are nearly all small, including only 3 zooids, and are rounded in shape. Later internodes become progressively more elongated and include more zooids; a typical sequence has 3, 6, 25, and 36 zooids. Occasionally, a small internode occurs later in astogeny, between two longer internodes. Zooid length at the base of an internode forms a series Lz 0·55, 0·47, 0·60, 0·55, 0·62, 0·58, 0·60 mm (cf. *E. obtecta*).

Brooding zooids appear by the fifth internode and are placed in the centre of a transverse zooidal series; a maximum of 10 occur in one internode. *T. burrowsi* is known from direct observation (Dr J.-G. Harmelin, *pers. comm.* 1974), to be a shallow-shelf species, and all the deep water records given above are of worn, dead internodes found in sediments which had been transported. The colonies from Madagascar were observed alive *in situ*; they have several epizoic and epiphytic forms, including sponges, small gorgonians, hydroids, serpulids, the bryozoan *Cellaria* sp. and small algae. The coelomic pigment of living colonies was bright red, and they were found growing together with gorgonians etc., and forming patches 20–40 cm across on calcareous accretions covered by sand.

NEOEUTHYRIS Bretnall

Neoeuthyris Bretnall, 1921 : 157.

TYPE SPECIES. *Euthyris woosteri* MacGillivray, 1891.

DESCRIPTION. Colonies encrusting, basal walls of zooids uncalcified except at the margins. Frontal shields curved, hyaline. Lateral walls prominent. Orifices with a wide sinus and paired condyles. Avicularia unilateral and oral, mandible hinged on a complete bar. Brooding zooids with large, dimorphic orifices and a brood chamber formed by a large endozooidal ovicell, closed by the operculum.

REMARKS. The characters of *N. woosteri*, the only species, differ from those of other genera of Euthyrisellidae in the encrusting habit, lack of basal coelom, and presence of ovicells and avicularia. The essential structure of the colony, the nature of the frontal shield, the interzooidal communications and the dimorphism of brooding zooids, are, however, all similar to those found in the other genera.

Neoeuthyris woosteri (MacGillivray)

Euthyris woosteri MacGillivray, 1891 : 77, pl. 9, fig. 2.
Neoeuthyris woosteri: Bretnall, 1921 : 158, Fig. 1. Hastings, 1960; 1964 : 245, figs 1, 2.

SPECIMENS EXAMINED. BMNH. Fremantle, Western Australia, 1948.3.12.1; Western Australia, 1938.8.10.1; Cosy Corner, Torbay Head, Western Australia, 1979.2.1.1.

AM and NMV: U875 HOLOTYPE (see Hastings, 1964 : 246).

DESCRIPTION (Figs 7, 12, 28, 29, 31, 32). *Neoeuthyris* encrusting algae (usually *Metamastophora flabellata*), zooid basal walls uncalcified. Zooids communicating by 3–5 lateral and 2–3 distal septulae placed at the base of the vertical walls. Visceral-to-hypostegal communication by paired groups of 4–5 septulae in the upper part of the distal

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Figs 10–13 Scanning electron micrographs of brooding zooids of Euthyrisellidae and Didymosellidae: (10) *Tropidozoum burrowsi* sp. nov. BMNH 1975.1.4.1, Madagascar ×103; (11) *T. cellariiforme* Harmer BMNH 1964.3.10.1, Celebes ×127; (12) *Neoeuthyris woosteri* (MacGillivray) BMNH 1979.2.1.1, Western Australia ×50; (13) *Didymosella larvalis* (MacGillivray) BMNH 1979.7.5.2, near Melbourne, showing partially formed ovicells at growing edge ×35.

wall behind the orifice (Fig. 32). Frontal shield smooth, very thinly calcified, with small protuberances, but no suboral septulae, and with no extension of hypostegal coelom basally. Two pairs of frontal septulae beside the orifice, one pair giving rise to an avicularium (Fig. 28). Avicularia with acute mandibles, directed proximally. Brooding zooids large, with dimorphic orifices, ovicell apparently formed by an expansion of the lateral and distal walls, protruding into the cavity of the next zooid, which is very short (Lz 0·45 mm).

REMARKS. Avicularia on the right hand side of a lobe tend to occur on the right hand side of the zooids (viewed frontally), and *vice versa*. The algal substratum is influenced during growth by the presence of the bryozoan (see Hastings, 1964).

The extreme fragility of the colonies makes investigation very difficult. Scanning electron microscopy of small fragments, and thin sections, have enabled us to reconstruct the interzooidal and intrazooidal communication systems, which are hardly visible in whole preparations using a light microscope.

N. woosteri has rarely been reported, and the ancestrula and early astogeny is unknown. Most specimens are known to have encrusted *M. flabellata* which had been washed up on the shore, and both species probably occur together in deeper water. Nearly all records are from Western Australia, but MacGillivray (1891) reported specimens from Cooktown, Queensland.

Table 2 Measurements (mm) of autozooids and avicularia of Didymosellidae

	Lz	lz	12o (av.)	Lr	Lm	No. of frontal pores
Didymosella sp. (Labracherie)	0·33–0·50	0·25–0·37	0·15	0·15–0·23	–	4
D. irregularis	0·58–0·73	0·34–0·37	0·22	0·14–0·22	–	10
D. acutirostris	0·50–0·60	0·50–0·60	0·16	–	–	–
D. crassa	0·68–1·00	0·69–0·90	0·27	0·22–0·27	–	30
D. porosa	0·50–0·75	0·33–0·44	0·15	0·08–0·13	–	10
D. clypeata	0·88–0·96	0·46–0·57	0·23	0·12–0·15	–	15
D. 'larvalis'-fossil (New Zealand)	0·50–0·60	0·45–0·48	0·16	0·20–0·30	–	9
D. 'larvalis'-fossil (Australia)	0·60–0·65	0·48–0·50	0·19	0·20–0·30	–	10
D. larvalis-Recent	0·55–0·70	0·40–0·50	0·18	0·20–0·30	0·15–0·25	10
D. parviporosa	0·55–0·75	0·35–0·65	0·16	0·13–0·20	–	20
D. pluma	0·65–0·80	0·64–0·90	0·22	0·28–0·32	0·70–0·80	20
T. magnirostris	0·80–1·00	0·60–0·80	0·15	0·25–0·28	0·23–0·30	20
T. magna	0·65–0·70	0·65–0·70	0·27	0·30–0·35	–	5
T. boninensis	0·60–0·90	0·50–0·70	0·20	0·15–0·20	0·50–0·75	15

DIDYMOSELLIDAE Brown

Didymosellidae Brown, 1952 : 194.

TYPE GENUS. *Didymosella* Canu & Bassler, 1917.

DESCRIPTION. Interior-walled cryptocystidean ascophorans, usually with extrazooidal basal coeloms, and considerable basal calcification. Zooid frontal shields with pores and marginal frontal septulae, becoming thickly calcified during ontogeny, obscuring the lateral walls.

Peristomes elongated, with or without foramina and/or spiramina frontally. Primary calcified orifice not well defined, operculum a flap-like extension of the distal part of the ascus wall. Septulae in vertical and basal zooid walls numerous. Avicularia adventitious, arising from oral frontal septulae, usually unilateral, with large subrostral chambers and acute rostra. Mandibles orientated laterally, hinged on a complete bar. Brood chambers formed by an expansion of the distal part of the peristome wall, opening above the operculum.

Ontogeny of zooid walls

As in the Euthyrisellidae, ontogenetic changes in the Didymosellidae are apparently rapid. Few colonies show complete series of frontal shield development, and partially uncalcified buds are contiguous proximally with fully formed zooids in which secondary calcification is well advanced (see Fig. 21). For a brief period, the prominent lateral walls and depressed crypyocystal shield resemble those of *Pleurotoichus* or *Tropidozoum*. The presence of numerous frontal marginal septulae, however, means that the frontal calcification soon thickens, obscuring all zooidal boundaries. Funnels in the calcification common to tubular extensions above septulae of adjacent zooids are developed, as in the umbonuloid genus *Tremogasterina* (see Cook, 1977).

The calcification of the primary orifice merges into the development of the peristome and no clear-out boundary is obvious. Avicularia are formed as lateral-oral frontal buds, their subrostral chambers deriving from a flattened plate of the frontal shield, bordered by 3–8 marginal septulae (see Fig. 20). In *D. pluma* particularly, funnels derived from these septulae, and frontal pores, remain prominent features of the large avicularian chambers quite late in ontogeny (see Fig. 21).

Coelomic systems and communication

The presence of frontal septulae is correlated both with the absence of interzooidal visceral-to hypostegal communication (Fig. 1B), and with the massive calcification of the frontal shields. In nearly all species, basal septulae, which communicate with a thin extrazooidal coelom, have been observed. Basal calcification, too, is considerable, and forms processes or massive pillars, which contact the substratum, allowing a semi-repent mode of life, or strengthening erect branches. The nature of the porous basal calcification has long been noted by authors (Stoliczka, 1865, MacGillivray, 1895, Waters, 1885, Levinsen, 1909, and Brown, 1952), who have either compared it to that of *Selenaria* (which also has an extrazooidal, basal coelom, see Chimonides & Cook, 1981), or have suggested a radicular function for the pores.

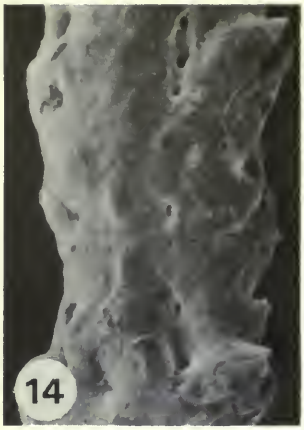
Opercula, mandibles and peristomes

In correlation with the elongated peristomes (see Harmer, 1957 : 652), and in contrast to the Euthyrisellidae, opercula are hardly differentiated, and are flap-like expansions of the ascus wall. Mandibles are acute, and hooked in *D. larvalis* and *T. magnirostris*. Those of *D. pluma* and *T. boninensis* are elongated and resemble the mandibles of the anascan genus *Smittipora* (see Harmer, 1926), in having a central rachis, and expanded wings of cuticle.

Brooding zooids

In some species, brooding zooids and their orifices are larger than those of autozooids, but there seems little evidence of dimorphism in other characters. In some species, the brooding zooids may have smaller avicularia, or none, and there is evidence of patterning of the avicularia of surrounding zooids.

Unlike the Euthyrisellidae, the family Didymosellidae has an extensive fossil record (see below).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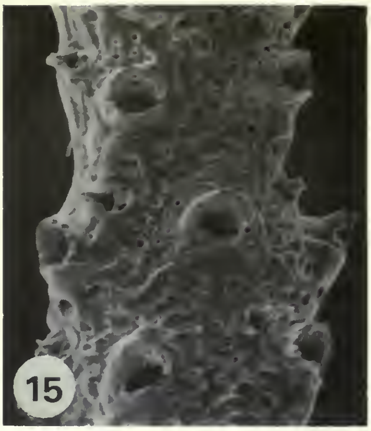
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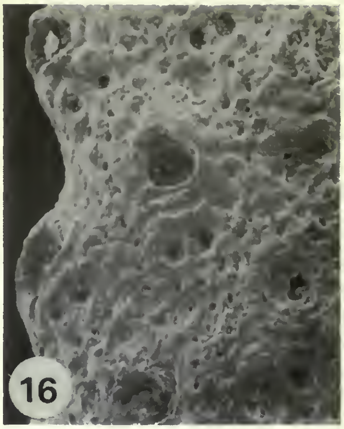
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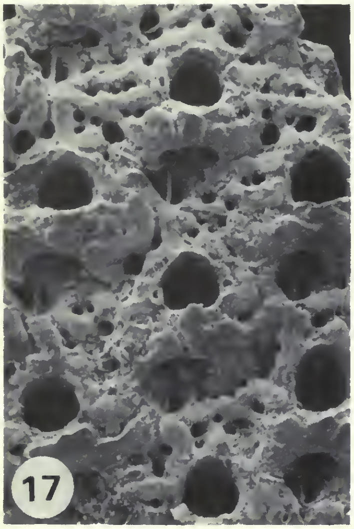
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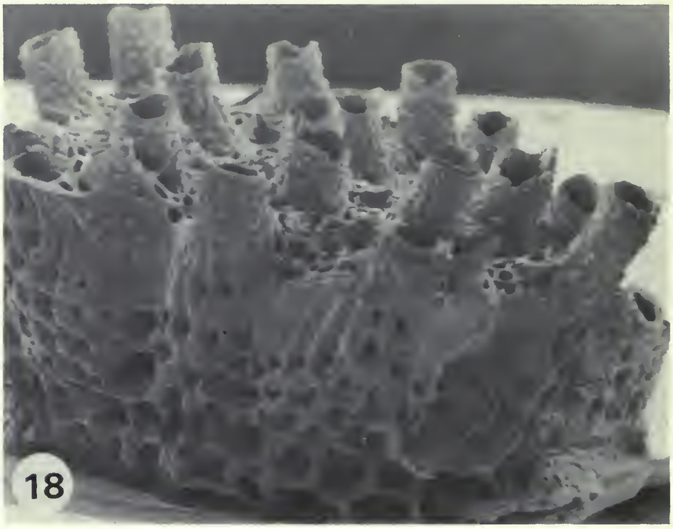
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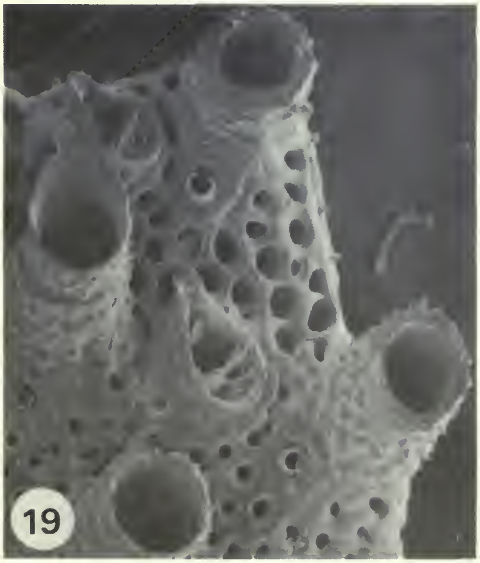
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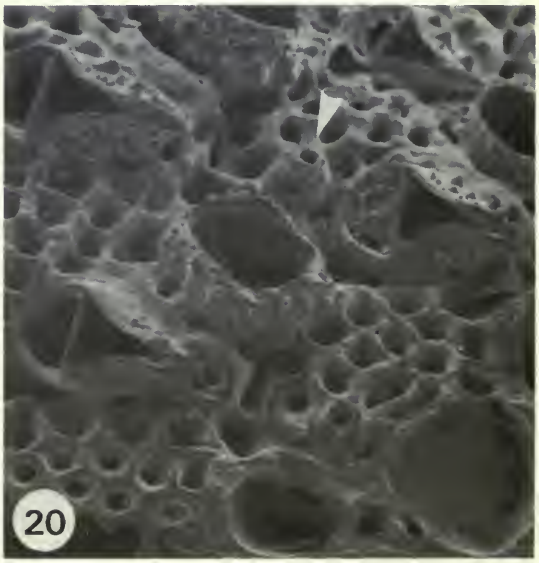
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DIDYMOSELLA Canu and Bassler

Didymosella Canu & Bassler, 1917 : 43.

TYPE SPECIES. *Lepralia larvalis* MacGillivray, 1869.

DESCRIPTION. Zooidal peristomes with large, paired foramina, spiramina absent.

REMARKS. *Didymosella* was included in the family Escharellidae by Canu & Bassler (1929 : 33), and in the Exochellidae by Bassler (1953 : G205). The distinctive characters of the genus were discussed by Brown (1952 : 194), who noted that the Italian fossil species *Porina bioculata* Waters (1891 : 26, pl. 3, fig. 15), the type species of *Bimicroporella* Canu (1904 : 12), was not closely related to *Didymosella. B. bioculata* (Waters), *B. ventricosa* Canu (1904) and *B. watersi* Brown (1958) all have some superficial similarity with *Didymosella*, but have no suggestion of a basal coelom, and have hyperstomial ovicells.

Didymosella has an extensive fossil record. The earliest known species is an undescribed form listed by Labracherie (1972 : 44), from the Middle Eocene of North Aquitain, France. Specimens of this species have been examined (Bazas-rural, 200 metres, Labracherie Coll.). The material is fragmentary and comprises only 30 zooids. Most of the fragments appear to have been encrusting, but some have basal grooves and a few have minute pores, which together with the thick, basal calcification are interpreted to indicate the former presence of a basal coelom. The frontal shields have 3–6 pores and 7–9 funnels indicating frontal septulae. Zooids communicate through 1–2 distal, and 2–3 lateral septulae. The paired peristomial foramina are distinct, as are the avicularian rostra, some of which have a complete bar. The rostra are open terminally which, by analogy with *D. pluma* (see p. 76) probably indicates that the mandibles were elongated.

Another fossil species, *D. irregularis*, was described from the Upper Eocene (Lower Jacksonian) of north-western Florida by Cheetham 1963 : 66, pl. 2, fig. 13). This had unilaminar colonies and larger zooids with up to 20 frontal pores and very small, acute avicularia. The orifices of the brooding zooids; which had broken peristomes exposing the ovicells, were slightly dimorphic.

In view of Labracherie's (1972) records, it appears that *D. acutirostris* Faura y Sans & Canu (1917 : 90, pl. 7, figs 3–5), from the Upper Eocene of Monresa, Barcelona, is also attributable to *Didymosella*. The illustration is not conclusive, but the species was described with paired, peristomial foramina and peristomial ovicells. The zooids were larger than those of Labracherie's species.

The wide Eocene distribution of *Didymosella* continued during the Oligocene and Miocene (see below), and is maintained in Recent seas.

Didymosella crassa Canu and Bassler

Didymosella crassa Canu & Bassler, 1920 : 116, pl. 88, figs 1–7.

SPECIMENS EXAMINED. BMNH. Oligocene (Vicksburgian), west bank of Conecuh River, Escambia Co., Alabama. Canu & Bassler Coll.

Figs 14–20 Scanning electron micrographs of fossil and Recent Didymosellidae: (14) *Didymosella clypeata* Canu & Bassler BMNH Lower Miocene, Victoria, basal side of branch, showing septulae ×31; (15) *D. clypeata*, frontal side of branch ×34; (16) *D. porosa* (Stoliczka) BMNH D 36784–92, Middle Oligocene, New Zealand, part of frontal margin of branch ×21; (17) *D. 'larvalis'* BMNH D36783-7, Miocene, New Zealand, ×40; (18) *Tubiporella boninensis* Borg BMNH 1889.8.21.105, Recent, China Sea, lateral view of young colony, ancestrula at right, showing basal extrazooidal calcification ×25; (19) *T. boninensis* zooids at growing edge, showing spiramina, frontal pores and avicularian rostra ×57; (20) *T. magnirostris* (MacGillivray) BMNH 1899.7.1.2686, Recent, Victoria, zooids viewed from distal end, showing spiramen (arrowed) and base of avicularian subrostral chamber (bottom right) ×57.

DESCRIPTION (Fig. 23). *Didymosella* with large zooids and tubular peristomes. Zooids with 25–35 frontal pores and 6–8 marginal septulae. Avicularia large, with channelled rostra open terminally. Basal surface thickened, with grooves and pores.

REMARKS. In all respects *D. crassa* and *D. pluma* (see p. 76) are so alike that it is possible to postulate a direct genetic link between the Oligocene and Recent populations from the central West Atlantic. The skeletal characters differ from those of *D. pluma* only in the larger number of frontal pores and in the absence of elongated calcified basal processes, which last may be due to wear during preservation. The open channel at the terminal end of the avicularian rostrum allows the inference that the mandible was elongated, and may have even been expanded laterally like that of *D. pluma* (see p. 78).

Didymosella porosa (Stoliczka)

Semiescharipora porosa Stoliczka, 1865 : 128, pl. 19, figs 10–13.
Didymosella porosa : Canu & Bassler, 1929 : 328.
Didymosella aff. *porosa* : Brown, 1952 : 198, Figs 139, 140.

SPECIMENS EXAMINED. BMNH. Middle Oligocene, Pareora, Tarahoke Quarry, N.W. tip of South Island, New Zealand, D36788-92.

DESCRIPTION (Figs 16, 27). *Didymosella* with erect, ligulate branches, with 4–5 transverse zooid series. Branches flat and bifurcated. Lateral marginal zooids curved outward, their peristomes forming serrations. Secondary orifices with paired spine bases. Marginal avicularia large. Basal calcification with numerous pores.

REMARKS. Branches are composed of 20 sequentially distal zooid series. The marginal zooids are curved so that their orifices are at an angle of over 45° to those of the central series. At the same time, the orifices are curved towards the frontal side of the branch. The paired peristomial foramina are separated from the proximal edge of the peristome by a distance greater than 0·20 mm.

Stoliczka (1865) mentioned the thickening of the basal calcification and the porous surface, which was also noted by Brown (1952), who suggested that the pores might have a radicular function. In spite of Brown's doubtful assignment of his material to *D. porosa*, it is so close in general characters, age and locality to Stoliczka's specimens (which were from the Lower Miocene of Orakei (Hauraki) Bay, North Island), that it may be confidently included in the species.

Didymosella clypeata Canu & Bassler

Didymosella clypeata Canu & Bassler, 1935 : 32, pl. 9, figs 7, 8.

SPECIMENS EXAMINED. BMNH. Lower Miocene, Mount Martha, Victoria. Anticline Creek (Janjukian), Dartmoor, Victoria D34200–01.

DESCRIPTION (Figs 14, 15). *Didymosella* with erect ligulate branches, with 2–3 transverse series of zooids. Branches curved towards the basal side so that orifices of the marginal series are at an angle of 70° to those of the central series. The marginal zooids also curve outwards slightly at about 15° to the central axis. Secondary orifices with paired spine bases. Frontal pores are stellate (in basal view) and the paired peristomial foramina are close to the proximal edge of the peristome, at a distance of 0·10–0·15 mm. Basal calcification thickened, with a few irregularly spaced pores.

REMARKS. The marginal avicularia are large, and occur about half way up the zooids.

Although very similar to *D. porosa, D. clypeata* differs in the number of zooids in a transverse series, the curvature of the branches and the placing of the peristomial foramina.

The combination *Porina clypeata* Waters (1881 : 332, pl. 17, fig. 67, 1882a : 268) was used for an entirely different species from the Miocene of Mount Gambier, Victoria.

The *Didymosella larvalis*–complex

The Recent species *D. larvalis* is here confined to algal-associated, encrusting colonies, with no evidence of basal coeloms. Two fossil populations, one from the Australian Miocene, the other from the Oligocene to Miocene of New Zealand, have been ascribed by several authors to *D. larvalis*. Neither of these populations is assignable to *D. clypeata* or *D. porosa*, and they differ considerably from Recent *D. larvalis* in their colony forms.

A. ***Didymosella*** aff. ***larvalis*** (fossil specimens)

Porina larvalis: MacGillivray, 1895 : 104, pl. 14, fig. 26, Waters, 1882a : 269, pl. 8, fig. 19; 1882b : 509; 1887 : 189, pl. 6, fig. 8.
Didymosella larvalis: Brown, 1952, part: 195, Figs 135–138; 1958 : 56.

Specimens examined. BMNH. Oligocene, Tarakohe Quarry, Waitapu, New Zealand, D36787; Miocene, Weka Pass, New Zealand, D36783–6, D36938, D36961–2; Miocene Muddy Creek, Victoria, Australia, D34255; Mount Gambier, Victoria, D32981–3 (Waters Coll.).

MM. Bairnsdale, Victoria, T42 (figured Waters, 1882a, pl. 8, fig. 19).

Description (Fig. 17). *Didymosella* with erect colonies with bilaminar expansions or cylindrical branches. Peristome slightly raised, thickened proximally forming a transverse ridge which overhangs the paired, peristomial foramina. Frontal pores stellate.

Remarks. The bilaminar colonies (from Weka Pass, New Zealand), have basal walls forming a double layer. No pores connecting the layers can be seen. The erect fragments also have complete basal walls, and have a central cavity. One fragment (D36786) has a very long avicularium with a channelled rostrum which is open terminally. In general, the specimens are poorly preserved and worn. The calcification is, however, considerably thicker than that of Recent specimens. The stellate frontal pores can be seen from the inner surface of broken zooids.

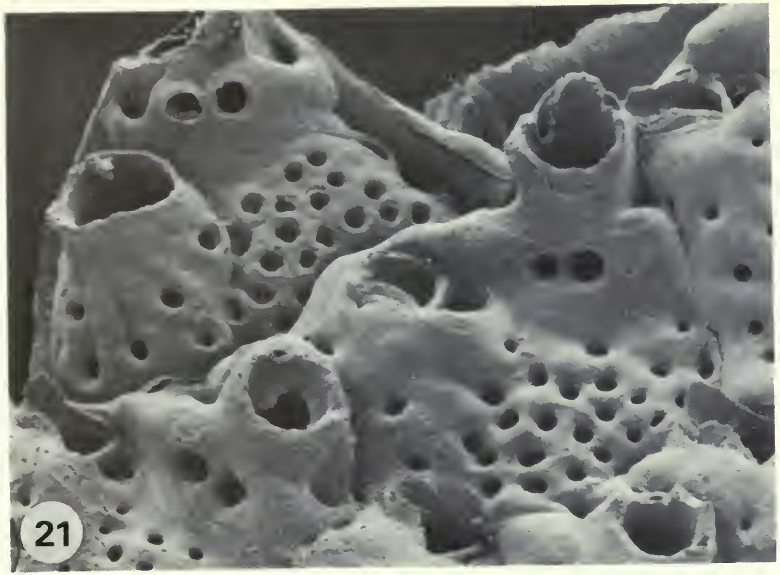
B. ***Didymosella larvalis*** (MacGillivray)

Lepralia larvalis MacGillivray, 1869 : 134. 1879 : 30, pl. 37, fig. 5.
Escharoides larvalis: Levinsen, 1909 : 318. Livingstone, 1926 : 170, pl. 11.
Didymosella larvalis Brown, 1952, part: 195.

Specimens examined. BMNH. Spencer Gulf, 1890. 4.17.10pt. Australia, 1897.5.1.883, 1963.4.18.16; Port Phillip Heads, 1897.5.1.881.882; Adelaide, 1899.7.1.5036A; Cowes Phillipps Id., 20 miles S.E. Melbourne, beach sand, 1979.7.5.2; No locality, 1963.2.12.63.

Description (Figs 9, 13, 36). *Didymosella* with colonies encrusting algae, sometimes rising into small, unilaminar expansions. Zooids communicating by 2 distal and 2–3 lateral multiporous septulae, surrounded by chambers of calcification. Basal wall uncalcified in encrusting zooids, peripherally calcified, or with a large, uncalcified, cuticle covered window in erect zooids. Proximal side of peristome elongated, calcification thin and hyaline. Distal side of peristome deficient. Lateral peristome with spinous processes. Frontal pores stellate, frontal septulae numerous. Avicularia large, with acute mandibles, hooked terminally. Ancestrula with a complex frontal shield of spinous processes.

Remarks. The thin frontal calcification and lack of basal calcification are similar to that of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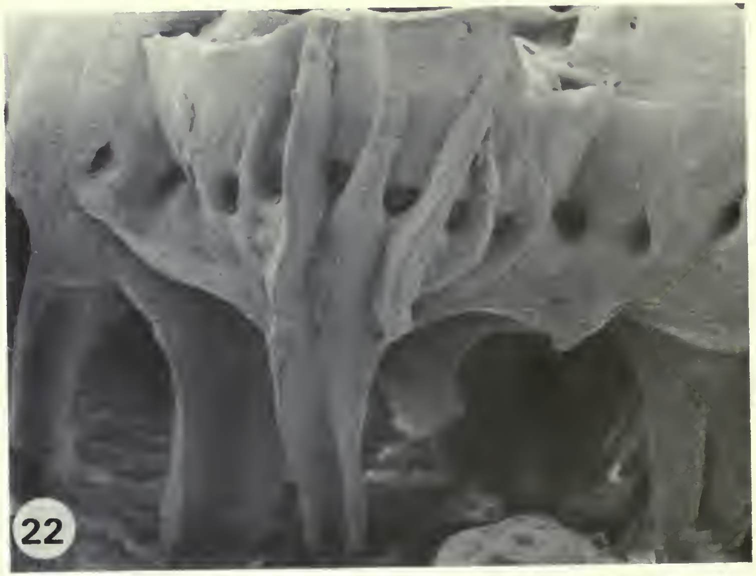
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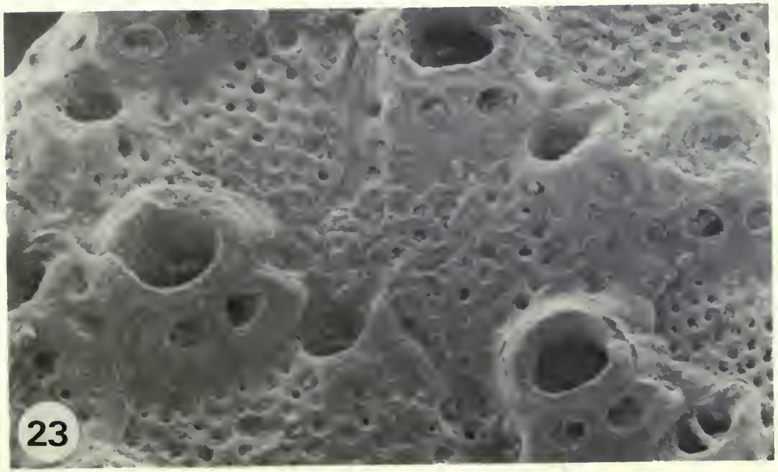
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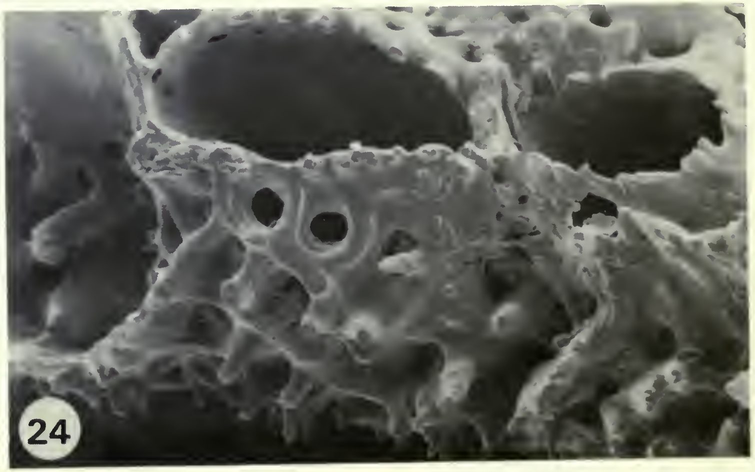
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the algal-associated *Neoeuthyris woosteri* (see p. 67), and are also usually present in numerous other cheilostome species which are specific to this type of substratum. In erect zooids, the uncalcified basal area is progressively decreased with astogeny, eventually becoming confined to a window in the basal wall. No evidence of a basal coelom or of radicular expansions has been seen.

Specimens are small, but a few parts of colonies (1897.5.1.882) comprising more than 100 zooids, on narrow fronds of algae, show a distinct central zone of brooding zooids which have minute, paired avicularia. They are flanked by lateral series of autozooids in which most of the avicularia are placed with the closed mandible directed medially (cf. *T. magnirostris*, p. 77). In other colonies, there is no obvious patterning of brooding zooids or of avicularia.

Ancestrulae (1890.4.17.1.–10 pt., 1963.2.12.63) are large (La 0·52 mm, la 0·40 mm), and distinctly 'cribrimorph' in character. There is a well developed gymnocyst and large, oval opesia, overarched by 4 robust lateral spines. The oral shield is formed by a pair of large, spinous processes, which are fused centrally, leaving an open foramen. The shield terminates distally in 5 spines, and a further, laterally placed pair of bifurcated spines is closely apposed to the lateral walls of the ancestrula and the distal-lateral primary zooids of the post-ancestular triad (see Fig. 9). The systematic significance, if any, of 'cribrimorph' ancestrulae in ascophoran species is unknown. The ancestrulae of other species of *Didymosella* have not been found, and that of *Tubiporella boninensis* (see below) is not 'cribrimorph', but resembles subsequent zooids. Most cribrimorph species have anasciform, 'tata' ancestrulae, but 'cribrimorph' ancestrulae are known in the umbonuloid ascophorans *Triporula bidenticulata* (Canu & Bassler), see Cook (1967 : 341) and *Romancheina asymmetrica* Moyano (1975 : 63, Figs 1–8). *Temachia opulenta* Jullien (1883 : 509, pl. 14, figs 26–29) also has a 'cribrimorph' ancestrula and is so similar to *R. asymmetrica* that it too may be postulated to have umbonuloid ontogeny. Apart from *D. larvalis*, the only cryptocystidean species with 'cribrimorph' ancestrulae known at present is *Schizoporella kiiensis* (Okada & Mawatari), see Mawatari (1952 : 279, fig. 13).

Didymosella parviporosa Canu & Bassler

Didymosella parviporosa Canu & Bassler, 1929 : 327, pl. 39, fig. 1.
Didymosella costulata Canu & Bassler, 1929 : 327, pl. 39, fig. 2.

Specimens examined. BMNH. Philippines, Albatross Stn D5145, 42 metres, 1931.12.30.119 (*D. parviporosa*); Stn D55141, 53 metres, 1931.12.30.120. (*D. costulata*).

Description. *Didymosella* with small, narrow zooids, each with an average of 20 frontal pores. Secondary thickening forming interzooidal funnels, with bars of calcification. Basal calcified wall with furrows and a few scattered pores. Avicularia, small, with acute rostra.

Remarks. The specimens include one fragment of *D. costulata* and three of *D. parviporosa*, together comprising only 40 zooids. Both species were described from the same region and *D. costulata* appears to be a slightly worn, ontogenetically thickened stage of development of *D. parviporosa*. This conclusion is strengthened by the locality data of the BMNH specimens, which were labelled by Bassler. One, labelled *D. parviporosa*, is from Stn 5145, the original locality for *D. costulata*; the other labelled *D. costulata*, is from Stn 5141, one of the original localities for *D. parviporosa*.

Figs 21–24 Scanning electron micrographs of fossil and Recent Didymosellidae: (21) *Didymosella pluma* sp. nov. BMNH 1899.7.1.5324, Recent, off Brazil, zooids at growing edge, showing raised lateral walls, frontal pores and channelled avicularian rostra ×71; (22) *D. pluma*, lateral view of zooids showing lateral septulae and basal calcified processes ×62; (23) *D. crassa* Canu & Bassler BMNH Oligocene, Alabama, showing channelled avicularian rostra ×59; (24) *Tubiporella magnirostris* (MacGillivray) BMNH 1899.7.1.2686, Recent, Victoria, growing edge viewed from distal end of zooids, showing distal and basal septulae and basal calcified processes ×75.

D. parviporosa differs from *D. larvalis* in the presence of a basal coelom, and its small, narrow zooids. It differs from *D. pluma* in its much smaller zooid size, and in its avicularian mandibles, which may be inferred to have been acute.

Didymosella pluma sp. nov.

Didymosella sp. Brown, 1952 : 198. Cook, 1981 (in press).

SPECIMENS EXAMINED. BMNH. HOLOTYPE, John Adams Bank (=Victoria Bank, off Brazil, Approx. 21°S, 37°W, depth less than 183 metres), 1899.7.1.5322. Paratypes, 1899.7.1.5323, 5324, 4476, 4477, 176; Havana, 1911.10.1.1702, 146 metres.

ETYMOLOGY. *Pluma* (L)—a feather, referring to the expanded avicularian mandible. The name was given as a manuscript label by Busk.

DESCRIPTION (Figs 21, 22, 25). *Didymosella* with semi-repent colonies forming irregular expansions. Frontal shield with 15–23 pores and 6–8 marginal septulae, the distal pair enlarged. Zooids communicating by 2–4 distal and lateral septulae. Peristomes raised, tubular, with paired, marginal spinous processes. Basal calcified wall becoming extrazooidal with septulae and long, calcified extensions. Avicularian subrostral chambers very large, rostra with a channel open terminally. Mandible very long, expanded and fimbriated laterally.

REMARKS. The thickening of the frontal calcification above and around the distal pair of frontal septulae forms large, slit like foramina, one either side of the orifice. Two large lobes of about 300 zooids each, show areas in which groups of zooids with 'left-handed' avicularia are opposed to groups with 'right-handed' avicularia. Unlike the colonies of *T. magnirostris* (see p. 79), these groups are not obviously associated with the presence of brooding zooids. The avicularian rostra have pores which are visible late in ontogeny. The remarkable mandibles resemble those of *Smittipora* (see Cook, 1964), but are fimbriated marginally. When open, each mandible covers the frontal foramina of the zooid; when closed, it usually covers the foramina of the adjacent, lateral zooid (see Fig. 25). Presumably the mandibles ensure that the foramina do not become blocked by detritus, which would restrict water flow into the ascus, and the laterally directed water currents produced by mandibular movement may assist in clearing deposits from the frontal surface of the zooids (see Cook, 1981). Expanded mandibles are also present in *Tubiporella boninensis* (see below).

D. pluma is so similar to *D. crassa* that it is highly probable that Miocene-to-Pliocene specimens, linking the two forms may eventually be found from sediments in the Gulf of Mexico region.

TUBIPORELLA Levinsen

Tubiporella Levinsen, 1909 : 304.

TYPE SPECIES. *Lepralia magnirostris* MacGillivray, 1883.

DESCRIPTION. Colonies semi-encrusting, with free expansions. Zooids with long, tubular peristomes and a frontal spiramen. Frontal and basal septulae numerous, and extrazooidal calcification considerable. Avicularia lateral, arising from several frontal septulae, subrostral chambers large. Rostra acute, directed laterally, mandible slung on a complete bar. Brooding zooids with a slightly enlarged orifice.

REMARKS. *Tubiporella* was introduced with no formal description. Levinsen (1909 : 304) listed it as 'n.g.' in a key to the family Tubucellariidae; *T. magnirostris* was the only species included. Species of *Tubucellaria* (or *Margaretta*, see Harmer, 1957 : 824), have an ascopore, not a peristomial spiramen, and have erect, jointed colonies. *Tubiporella* was assigned to the Tubucellariidae by Bassler (1953 : G210), and to the Porinidae by Harmer

(1957 : 844). Finally, Brown (1952 : 194) recognized its close affinities with *Didymosella* and included it in the family Didymosellidae.

Tubiporella, like *Didymosella*, has an Australian Tertiary record, although this extends only to Miocene deposits. The characters of fossil specimens are very similar to those of Recent *T. magnirostris*, but there are some doubts in accepting the identity of these forms without examination of type specimens. Brown (1952) noted that Recent colonies had the larger zooidal dimensions (see Table 2), and in view of the degree of difference between Recent and fossil populations of the *D. larvalis*-complex, it seems advisable at present to regard the Tertiary forms as distinct taxa. Several fossil forms have been described. Waters (1882*a* : 268, pl. 9, figs 33, 34) introduced *Micropella introversa* from the Miocene of Mount Gambier, Australia with two drawings which he stated were magnified at ×12 and ×25 respectively. The (secondary) orifice measurements he gave on p. 268 were: Lo 0·16 mm, lo 0·20 mm. Using the magnifications given, the average dimension of zooids for Fig. 33 would be: Lz 1·75 mm, lz 1·00, Lo 0·25 mm, lo 0·33 mm. These are obviously too large; very few cheilostome zooids are more that 1·5 mm in length, and Waters did not mention that the zooids of *M. introversa* were particularly large. A magnification of ×20 would give Lz 0·90 mm, lz 0·60 mm, Lo 0·15 mm, lo 0·20 mm, which is not only in accordance with the given orifice measurements, but is more feasible. The spiramen, which Waters regarded as 'microporellid' ascopore, was described and figured as being very close to the proximal border of the secondary orifice. When describing further fossil specimens from the River Murray Cliffs, Waters (1885 : 296) called this a 'central pore'. In a still later paper, Waters (1887 : 55) included *M. introversa* in the synonymy of *T. magnirostris* although the species had originally been described by him a year before MacGillivray's species. Waters (1885 : 295, pl. 7, fig. 7) also described, as *Microporella magna*, fossil specimens from Aldinga and Mount Gambier, and identified them with *Lunulites magna* Tenison Woods (1880), which he stated was 'very closely allied' to *T. magnirostris*. Tenison Woods (1880 : 7, pl. 1, figs 6 a–d), had described an irregularly domed, hollow, almost circular colony. His figure (6c) shows zooids with raised peristomes, numerous frontal pores and acute, laterally directed avicularia with a complete bar. This species is obviously ascophoran, and is in no way referable to the free-living, anascan genus *Lunulites*. Two specimens in the British Museum Collections confirm the existence of this species in the Australian Tertiary. The first (labelled '*Lunulites magna*'. D33050, Janjukian, Aldinga) has a domed colony 25 mm in diameter and 10 mm high, somewhat larger than Tension Woods' colonies. The zooids have raised peristomes, extrazooidal frontal thickening with funnels and pores, and a distinct proximal pore which may be a spiramen. The avicularia are directed almost distally, and are much larger than those figured by Tenison Woods (1880, pl. 1, fig. 6c). They have a complete bar, and the rostra are acute, with a terminal channel which may indicate that the mandibles were elongated. The basal surface of the colony is obscured by matrix. The second colony (D31940, River Murray Cliffs) forms an almost truncated cone 20 mm in diameter and 13 mm high, but the zooids are not arranged in regular radial series. They are very worn, but the peristomial orifices and avicularia can be seen. The hollow basal side of the colony has numerous pores and irregular masses of calcification and may be inferred to have possessed an extrazooidal coelom in life.

Pachystomaria parvipuncta MacGillivray (1895 : 97, pl. 8, fig. 24), another Miocene Australian form, appears to be a further species belonging to this complex. MacGillivray noted that the porous basal surface was similar to that of *Selenaria*, an observation also made by Waters (1885) when describing *M. magnirostris*. At present it is not known whether any or all of these nominal species are synonymous, or if they are conspecific with Recent *T. magnirostris*.

Tubiporella magnirostris (MacGillivray)

Lepralia magnirostris MacGillivray, 1883 : 134, pl. 1, fig. 6.

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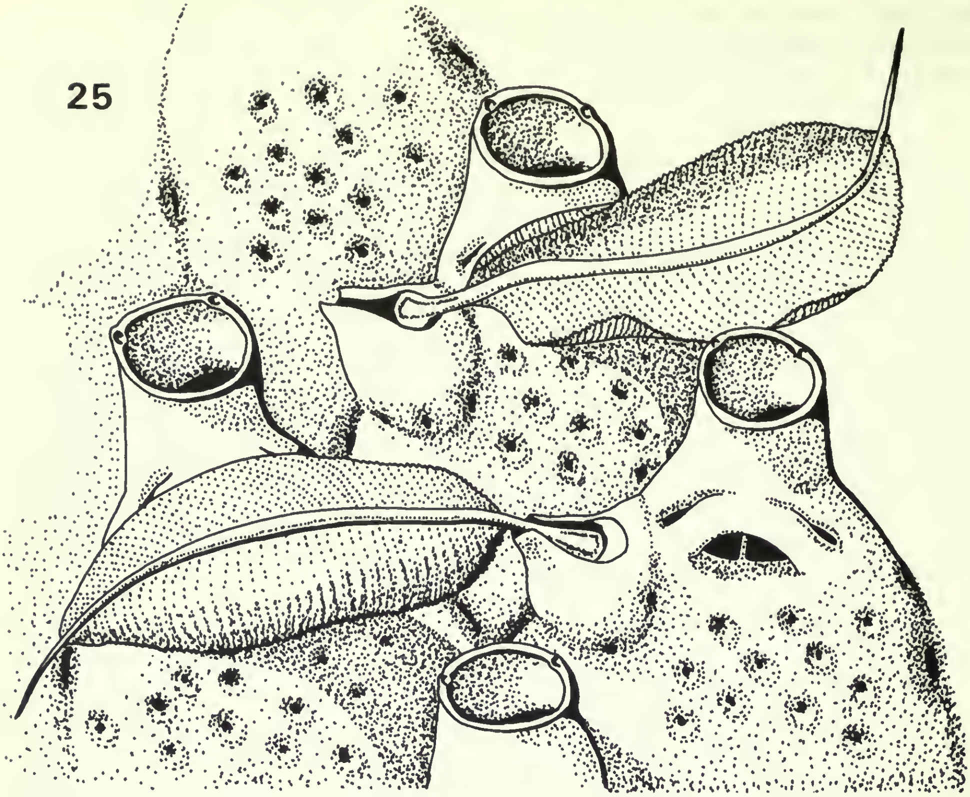

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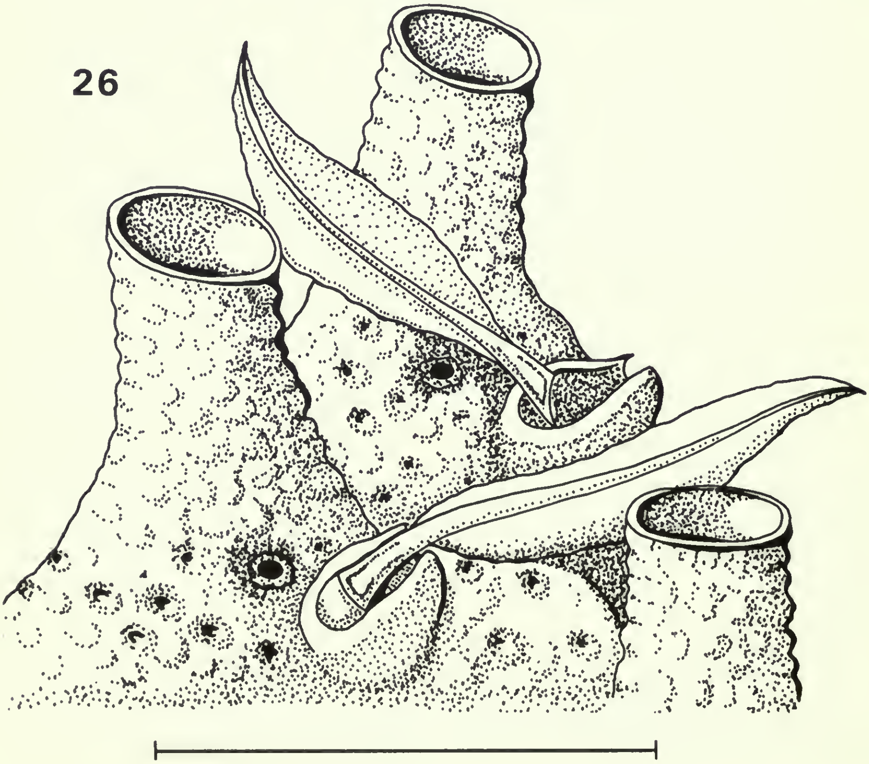


Tessaradoma magnirostris: MacGillivray, 1889 : 211, pl. 175, fig. 1.
Porina magnirostris: Hincks, 1884 : 279 (sep. p. 129), pl. 9, fig. 6.
Tubiporella magnirostris: Levinsen, 1909 : 307, pl. 16, figs 5a–d. Canu & Bassler, 1920 : 549, Figs 161 A–D.
Tubiporella magnirostris part, 'f. *victoriensis*': Borg, 1940 : 416, Figs 1–3.

Specimens examined. BMNH. Port Phillip Heads, Victoria, Australia, 1887.6.27.1, 1887.12.10.120, 1893.8.11.17, 46 metres; 1927.8.4.24, 1979.1.12.3. Port Phillip, 1899.5.1.1214, 1899.7.1.5409, 5410, 5411, 2333, 2338, 2686, 2687, Victoria, 1979.7.2.1. Amirante Islands, 64 metres, 1936.12.30.199.

NMV. Port Phillip, 63876.

Description (Figs 20, 24). *Tubiporella* with colonies forming broad, foliaceous expansions attached above the substratum by thick, extrazooidal, columns of porous calcification. Zooidal peristomes tubular, but not very prominent, with a small proximal, cuticle-covered foramen early in ontogeny. Spiramen originating on the proximal edge of the base of the peristome, apparently migrating proximally with thickening calcification. Avicularian subrostral chambers without pores, mandible hooked but not greatly elongated. Lateral frontal septulae surrounded by large uncalcified areas, which increase in size with calcification. Brooding zooids with larger secondary orifices than autozooids, with no avicularia, or paired, small avicularia. Avicularian mandibles of autozooids surrounding brooding zooids are directed away from brooding zooid when closed.

Remarks. The primary orifice can be seen early in ontogeny, and the developing peristome has a small foramen which rapidly becomes obscured. The 'migration' of the spiramen with thickening of the frontal shield is similar to that described in the umbonuloid family Adeonidae (see Cook, 1973). The patterning of brooding zooids and avicularia is similar to that found in *D. pluma*. The peristomial orifices of the brooding zooids are slightly larger than those of the autozooids, and the distal expansion of the ovicell can be seen. The lateral frontal septulae of the brooding zooids remain visible at the base of the funnels in the calcification, resulting in wide lacunae beneath the investing cuticle (cf. *D. pluma*). Levinsen (1909 : 308) mentioned that the 'very thick basal wall of the colony . . . is . . . perforated by pore canals' which he noted were derived from multiporous basal septulae. Harmer (1957 : 1012) described a colony of *Emballotheca subimmersa* (MacGillivray) which encrusted the basal wall of a large specimen of *T. magnirostris*.

Tubiporella boninesis Borg

Tubiporella magnirostris part, 'f. *boninensis*': Borg, 1940 : 420, Fig. 4, (operculum).

Specimens examined. BMNH. Tizard Reef, 64 metres, 1889.21.27; 68 metres, 1892.8.8.26; Macclesfield Bank, China Sea, 66 metres, 1889.8.21.95,105; 64–79 metres, 1934.11.6.23; 46 metres, 1893. 8.11.17; China Sea, 66 metres, 1979.1.6.2; S. of Bua Bua passage, Falafuti, 264 metres, 1903.1.29.60. Fuafatu, 109 metres, 1903.1.29.61.

Description (Figs. 18, 19, 26). *Tubiporella* with narrow, ligulate, semi-erect colonies, with zooids in 4–7 transverse series. Zooids with long, tubular peristomes, imperforate early in astogeny. Spiramen at the base of the peristome, migrating only slightly with ontogeny. Basal calcification produced into a massive, central keel in erect specimens, which produce branched, supporting pillars of extrazooidal, porous calcification 5–7 mm deep. Avicularian subrostral chambers large, imperforate. Rostra acute, with an open channel terminally.

Figs 25 and 26 (25) *Didymosella pluma* sp. nov. BMNH 1899.7.1.5322, off Brazil, sketch of four zooids and two avicularia with open (upper) and closed (lower) mandibles. Scale bar = 0·50 mm; (26) *Tubiporella boninensis* Borg BMNH 1893.8.11.17, China Sea, sketch of three zooids and two avicularia with open (upper) and closed (lower) mandibles Scale bar = 0·50 mm.

Mandibles elongated, directed laterally towards the margins of the colony; expanded laterally, with notched, fimbriated edges.

REMARKS. Although Borg (1940) did not consider that his specimens were specifically distinct from *T. magnirostris* and did not formally introduce the name '*boninensis*' for them, the name is available and is therefore used here. Borg noted that the operculum was hardly differentiated from the ascus wall, and that the avicularian mandible was 'distinctly broader than that of the Australian colonies and nearly straight, but with its tip rather sharply bent'. He also described the cuticular expansions and noted that 'this border is often broader on one side'. The mandibles are similar to those of *D. pluma*; when open they cover the area above the frontal spiramen. (see Fig. 26).

The ancestrula resembles later-budded zooids and is unusual in having a lateral avicularium.

Generally, *T. boninensis* differs from *T. magnirostris* in its colony form, shorter, more erect zooids, longer peristomes, and avicularian mandibles.

Note on ***Tubiporella levinseni*** Borg, 1940

In his description of the genus *Tubiporella*, Borg (1940) described a new species, *T. levinseni*, which had large, encrusting zooids with long, tubular peristomes, multiserial marginal pores and a proximal spiramen. The centrally placed avicularium had an elongated, almost setiform mandible. Borg mentioned that he had shown his specimens to Sir Sidney Harmer, who had recognized them as belonging to the same species as specimens from the Paternoster Islands which were present in the Siboga Expedition Collections. Harmer was not aware of Borg's description, which was subsequently published in Sweden during the 1939–1946 war (see Explanatory Note by Dr A. B. Hastings in Harmer, 1957 : xiv). The specimens from the Paternoster Islands were described as *Reptadeonella flagellifera* by Harmer (1957), who, however, had provisionally labelled them as '*Tubiporella*'.

The structure and relationships of *T. levinseni* differ from those of *Tubiporella* as represented by the type species, *T. magnirostris*, and by *T. boninensis*. The specimens examined by Harmer from the Siboga Collections, together with one large, additional colony without locality, but comprising more than 2000 zooids (which was found fortuitously in the unnamed collections of the BMNH, and was not seen by Harmer), have been examined. A few zooids show a cuticular frontal wall with operculum, which is overarched by calcification, indicating that the ontogeny of the frontal shield is umbonuloid. There are no frontal pores, and the frontal septulae are multiserial and extend round the distal side of the orifice (see also Borg, 1940). The long tubular peristome is thus subterminal, and the primary orifice is well defined, wih minute condyles and distinct operculum (see also Borg, 1940 : 422, Fig. 8). The avicularium is central in position and is derived from one lateral-oral septula. The subrostral chamber is small, and the rostrum is acute and directed distally and laterally. The mandible is elongated, setiform and slung between condyles. Zooids communicate through septulae at the base of the vertical walls, but there is no basal coelom and the basal wall is completely calcified. The zooids are nearly all encrusting, but where they stretch across irregularities in the substratum, have produced small, peg-like expansions. There are however, no extrazooidal pillars as in *Tubiporella*.

All the character correlations are similar to those found in the umbonuloid family Adeonidae (see Cook, 1973), and they confirm that Harmer (1957) was correct in attributing his specimens to the genus *Reptadeonella*, which has encrusting colonies.

Both Borg (1940) and Harmer (1957) mentioned that some zooids with short peristomes may have been brooding zooids. A few zooids have wide, rather slit-like orifices, but their peristomes do not differ from those of other zooids. Generally, brooding zooids in the Adeonidae are strongly dimorphic, and it is probable that as yet, no brooding zooids have been found in this species. The synonymy, distribution and measurements of *R. levinseni* (Borg) are as follows:

Reptadeonella levinseni (Borg)

Tubiporella levinseni Borg, 1940 : 420, pl. 1 and Figs 5–8.
Reptadeonella flagellifera Harmer, 1957 : 817, pl. 54, figs 4–7.

SPECIMENS EXAMINED. BMNH. Siboga Stn 315, N. of Sumbawa, Paternoster Islands, 0–36 metres, 1979.1.2.1; no locality, 1979.1.2.2.

ZMA. Stn 315 and Stn 60, 303, Hangsisi, Samau Islands, W. Timor, 0–36 metres.

DISTRIBUTION. Jaluit, Marshall Islands, 2 metres (Borg), Paternoster Islands and West Timor.

MEASUREMENTS (in mm). Lz 0·80–1·30 lz 0·50–0·90 Lo 0·13 lo 0·16–0·20 Lr 0·16–0·25 Lm 0·30–0·50.

Discussion

Study of Bryozoa emphasizing the concept of colonies as entities composed of cooperative members has increased during recent years as a result of observation of living colonies and the application of new techniques. Species show many kinds and degrees of structural and functional integration. Colonies may be composed of almost autonomous member zooids, or have various correlations of morphology and behaviour which in some cases amount to virtual colony control (see Cook, 1979*a*, and Ryland 1979). The relationships of zooid body walls, intercommunications, zooidal and extrazooidal coeloms, astogenetic and ontogenetic changes, polymorphism and the patterning of polymorphs, all express the degree of such colony control and may be analysed and arranged in series of increasing integration (see Boardman & Cheetham, 1973 and Cook, 1979*a*).

Expressed in terms of such series, the degree of integration of the families Euthyrisellidae and Didymosellidae is considerable. It is reflected in the zonation and polymorphism of brooding and avicularian zooids, and in the supporting and attachment structures of colonies. Most significantly, it is expressed in the preponderance of interior calcified walls, and in the various combinations of intrazooidal, interzooidal and extrazooidal coelomic communications.

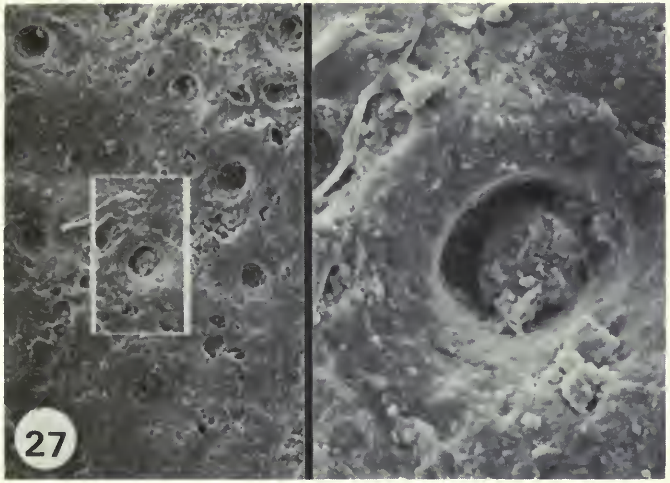
Relationships both between the Euthyrisellidae and the Didymosellidae, and between them and other ascophoran groups are hard to evaluate. Although they share cryptocystidean frontal shield ontogeny, the differences between the two kinds of shield suggest that these structures have arisen more than once in cheilostome evolutionary history. The appearance through time of more than one kind of frontal shield in the 'catenicellid' genera (see Banta and Wass, 1979), indicates that many more cryptocystidean families will require detailed investigation before the degrees and kinds of relationships among apparently similar groups are established.

The presence of extrazooidal basal coelom and of interior basal zooid walls is another shared character. However, these structures are also known in such diverse systematic groups as the lunulitiform, free-living anascan Selenariidae (see Chimonides & Cook, 1981) and the cryptocystidean Petraliidae. *Petralia undata* has erect, reteporiform, rooted colonies with a high degree of organization and an extensive basal coelom.

The lateral and basal rooting coleomic systems of the Euthyrisellidae have very close parallels among the many erect, flustriform genera, especially *Onchoporella* (see p. 59).

Peristomal spiramina, too, are found in a diversity of Recent and fossil ascophoran genera; for example, *Adeonella* (see Cook, 1973), *Gigantopora* (see Harmer, 1957), and compare *Pachydera rarepunctata* Voigt (1967 : 67, pl. 24, figs 1, 2, from the Upper Cretaceous of West Kasachstan, USSR).

Within the Euthyrisellidae, there is great diversity in frontal shield calcification and in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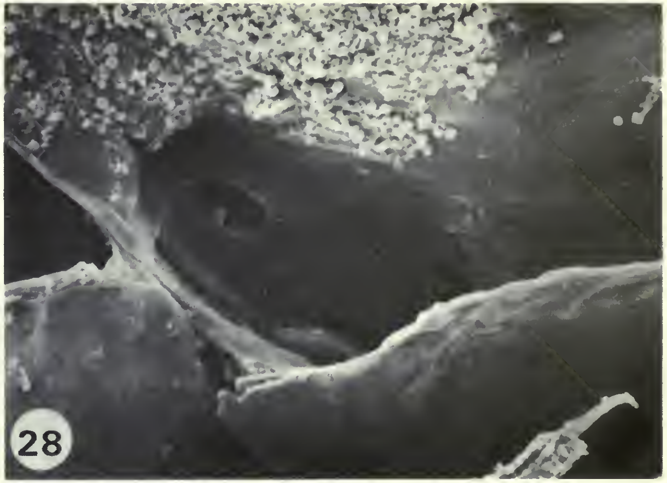
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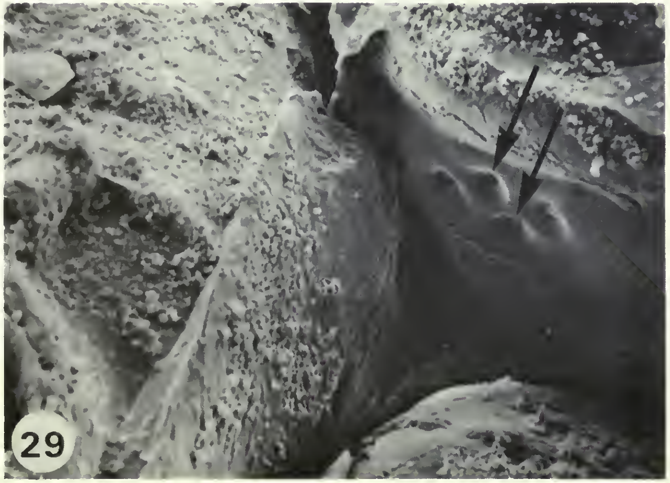
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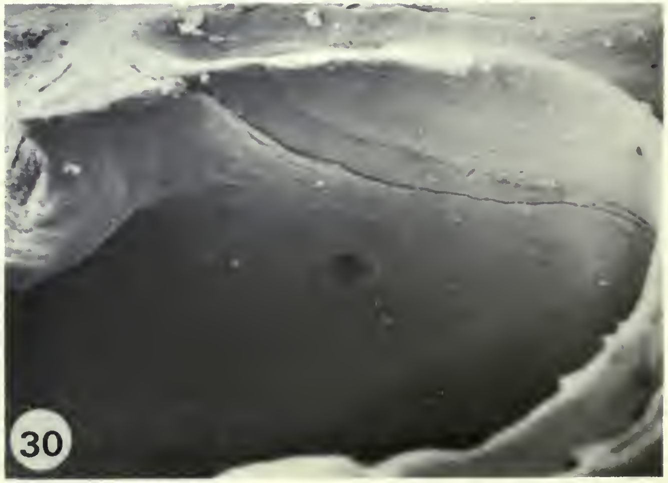
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orifice shape which is not strongly correlated with colony form. This diversity suggests that the family has a long evolutionary history, but unfortunately, no fossil species are known. Internodes of *Tropidozoum* are fairly robust, and have been found in transported deposits; they might be expected to be recognizable in Tertiary sediments. Even the thinly calcified zooids of *Euthyrisella* could be preserved, by analogy with the equally fragile fragments of *Selenariopsis*, which have been found, albeit rarely, in the fine fractions of Australian Miocene sediments (see Cook & Chimonides, 1981). Lagaaij (1968, 1973) has documented records of similar fragile species, several of which were not previously known as fossils. It is perhaps possible that the ancestral forms of Euthyrisellidae had more heavily calcified colonies, which have not yet been recognized as being systematically related to the Recent species.

In contrast, the long fossil record of the Didymosellidae might be expected to provide some evidence of evolutionary trends and relationships. Diversity among the known species, both in zooidal morphology and colony form is, however, far lower than that found in the Euthyrisellidae. Generally, the species have very similar patterning of avicularia and autozooids, and the repent or semi-encrusting colony form is know in both Eocene and Recent species. The erect, branching colonies of *D. porosa* and *D. clypeata* are not found among Recent species, and the algal association of *D. larvalis* (like that of *Neoeuthyris woosteri*), may have been evolved fairly recently.

To a certain extent, the distribution of species in time and space shows strong collection bias, and reflects the large number of faunal descriptions of the abundant bryozoan sediments of the Tertiary-to-Recent of the Gulf of Mexico and Australasian regions. The Euthryisellidae seems to have a purely Indo-West Pacific and Australian range. Most species are from shallow shelf or sublittoral waters, and several are rooted in sediments. The Didymosellidae are also shallow shelf species, although *D. pluma* and *T. boninensis* are found from the deeper end of the range. All species are from warm waters. Labracherie (1972) noted that the occurrence of *Didymosella* (together with other species) allowed the inference of warm marine conditions in the Middle Eocene of south Western France. The general pattern of distribution of the family in time and space follows that illustrated by Lagaaij & Cook (1973) for other warm water, shallow shelf species, and even for some deeper water forms (see Cook & Lagaaij, 1976). This comprises a very wide (sometimes circumtropical) distribution during the Eocene and Oligocene followed by a progressive restriction of range in a south-easterly direction through time. The occurrence of Recent *D. pluma* off Brazil and in the Gulf of Mexico is of importance, as it indicates that, like the genus *Adeonellopsis* (see Cook, 1973), groups which are supposed to be 'extinct' in the western Atlantic may be found to be still living in this area.

Summaries in French and German

Nous décrivons la structure de la colonie et la morphologie zooidale trouvées dans les deux familles cheilostome-cryptocystidiennes des Bryozoaires, la Euthyrisellidae et la Didymosellidae. Tous les murs calcifiés sont internes, at les coelomes basals (extra-zooidales) sont présents dans presque toutes les espèces. Dans la famille Euthyrisellidae, la communication interzooidale viscerale- à hypostigienne complémente ou meme remplace

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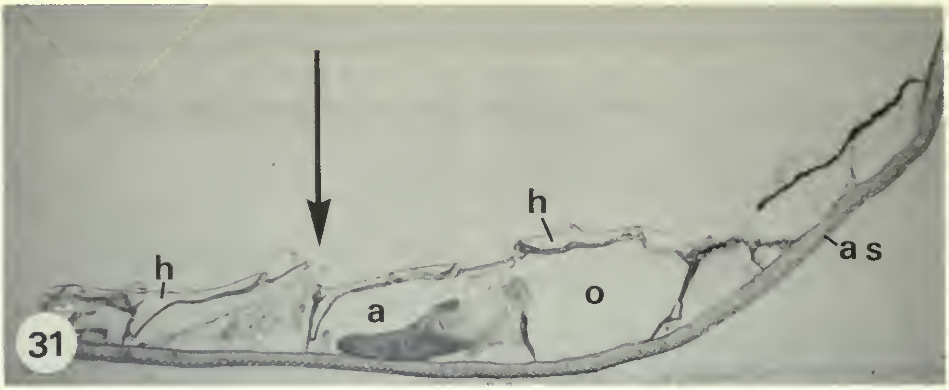
Figs 27 – 30 Scanning electron micrographs of communication septulae: (27) *Didymosella porosa* (Stoliczka) BMNH D36788–92, Middle Oligocene, New Zealand, basal septulae (left) ×100 (right) ×600; (28) *Neoeuthyris woosteri* (MacGillivray) BMNH 1979.2.1.1, Recent, Western Australia, lateral frontal septulae at base of developing avicularian subrostral chamber ×315; (29) *N. woosteri*, visceral-to-hypostegal septulae (arrowed) viewed from distal side ×197; (30) *Tropidozoum cellariiforme* Harmer BMNH 1964.3.10.1, Recent, Celebes, visceral-to-hypostegal septula in distal-lateral wall of brooding zooid, viewed from proximal side. Note suture in wall showing contribution of distal zooid calcification to brooding zooid orifice ×368.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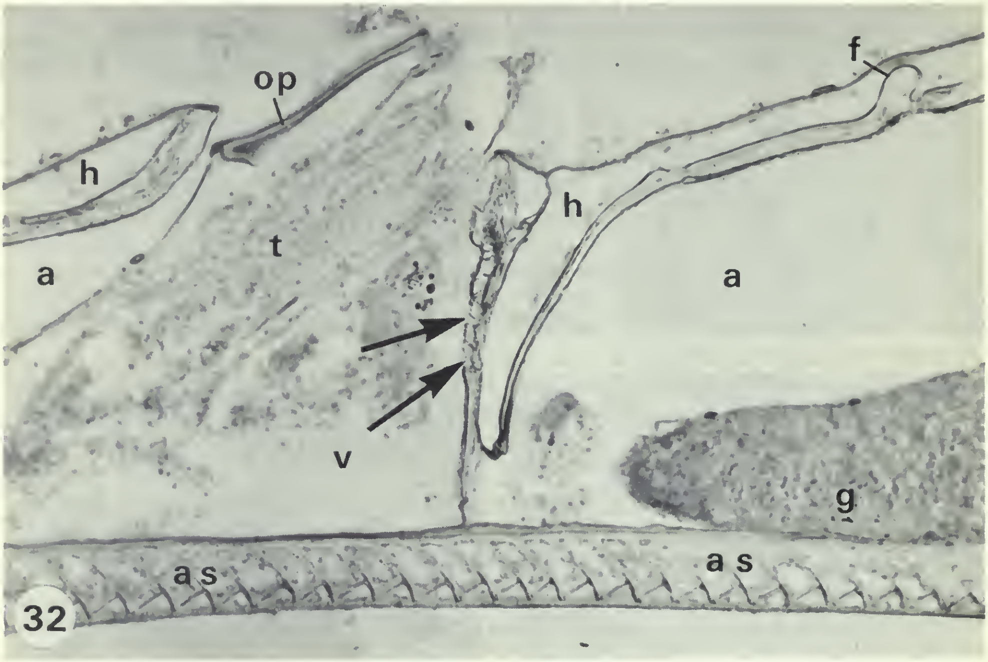
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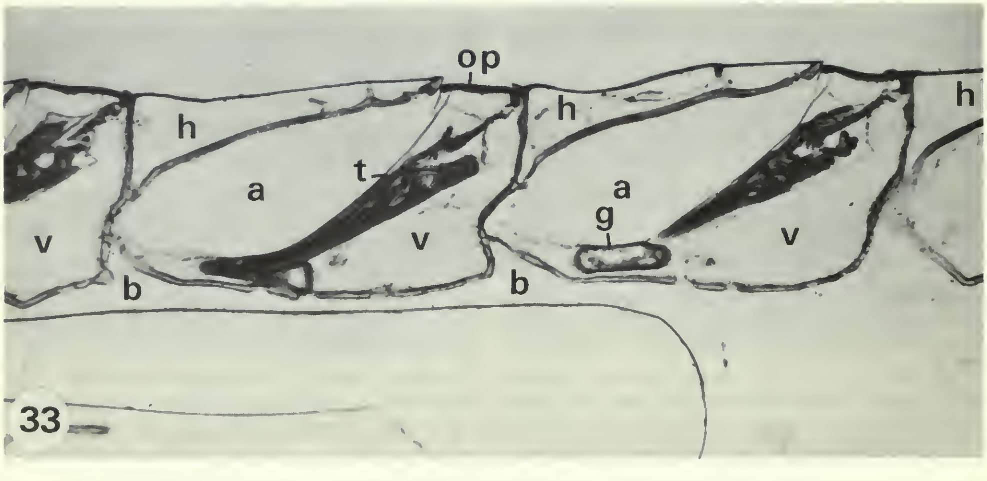
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la sorte intrazooidale la plus commune, cells qu'on trouve dans la Didymosellidae. Dans la Euthyrisellidae, une extension du coelome hypostigienne au-dessous du coté basal de la paroi frontale cacifiée, est présente dans la majorité des espèces. Une espèce nouvelle est introduite, *Tropidozoum burrowsi*. La famille Didymosellidae possède un record fossil qui s'étend d'Eocène Moyen et a une distribution très grande du Tertiare au Récent. Nous introduisons une nouvelle espèce Recente, *Didymosella pluma. Tubiporella boninensis* Borg a été redefinie. *Tubiporella levinseni* Borg a été redécrite et attribué au genre umbonuloide *Reptadeonella*.

Die Koloniestruktur und Morphologie der Zooide der Euthyrisellidae und Didymosellidae, zweier cryptocystider Familien der Bryozoa Cheilostomata, werden beschrieben. Alle verkalkten Wände sind intern, und kolonieweite (extrazooidale) Basalcoelome finden sich bei fast allen Arten. Bei den Euthyrisellidae ergänzt oder sogar ersetzt die interzooidale (viscerale bis hypostegale) Kommunikation die gewöhnlichere intrazooidale, die sich bei den Didymosellidae findet. Bei den meisten Arten der Euthyrisellidae ist eine Verlängerung des hypostegalen Coeloms an der Basalseite des verkalkten Frontalschildes zu beobachten. Eine neue Art, *Tropidozoum burrowsi*, wird eingeführt. Die Familie Didymosellidae ist fossil seit dem mittleren Eozän nachgewiesen und ist vom Tertiär bis zur Gegenwart weit verbreitet. Eine neue recente Art, *Didymosella pluma*, wird eingeführt und *Tubiporella boninensis* Borg neu definiert. *Tubiporella levinseni* Borg wird wiederbeschrieben und in die umbonuloide Gattung *Reptadeonella* verwiesen.

Acknowledgements

These investigations would not have been possible without the collection and donation to the British Museum (Natural History) of well-preserved specimens of 'rare' species. We are therefore particularly grateful to Dr P. Bock (Royal Melbourne Institute of Technology, Victoria), Dr J.-G. Harmelin (Station Marine d'Endoume, Marseille), Dr J. S. Ryland (University College of Swansea), Dr R. E. Wass (University of Sydney, New South Wales) and Dr W. J. Woelkerling (La Trobe University, Victoria) for their help. We should also like to thank Dr M. Labracherie (Université de Bordeaux) and Dr P. Taylor (British Museum, Natural History) for the loan of fossil specimens.

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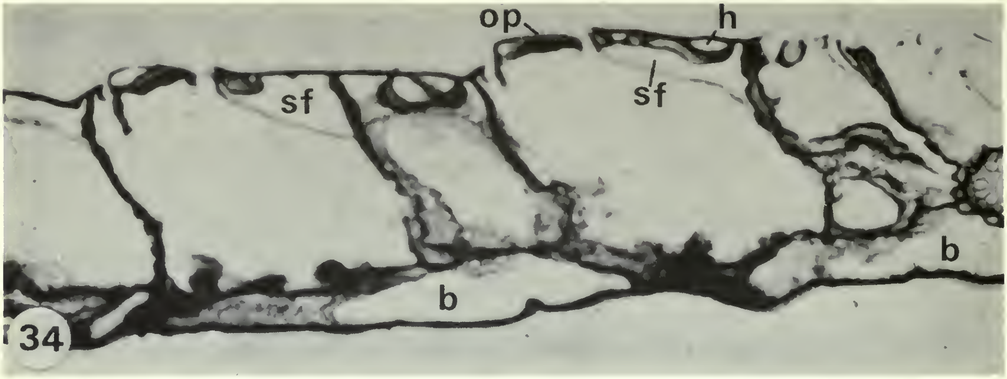
Figs 31–33 Micrographs of longitudinal thin-sections of epoxy resin embedded specimens of Euthyrisellidae: (31) *Neoeuthyris woosteri* (MacGillivray) BMNH 1979.2.1.1, Western Australia, zooids with cuticular basal walls encrusting algae, autozooid (left) and brooding zooid with large ovicell (centre), arrow indicates area enlarged in Fig. 32 ×30; (32) *N. woosteri* visceral-to-hypostegal communications (arrowed) ×165; (33) *Euthyrisella obtecta* (Hincks) BMNH 1890.7.23.38, Torres Straits, brooding zooids (without ova), cuticular basal wall detached at right ×70. *a* ascus, *o* ovicell, *op operculum*, *f* frontal process, *t* tentacles, *g* gut, *h* hypostegal coelom, *v* visceral coelom, *b* basal coelom, *as* algal substratum.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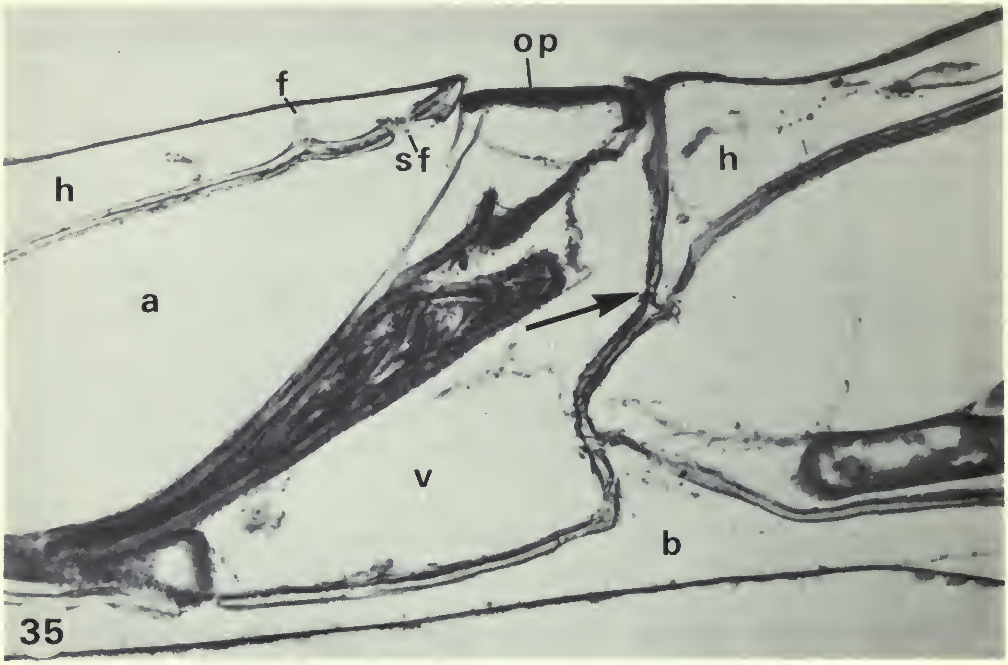
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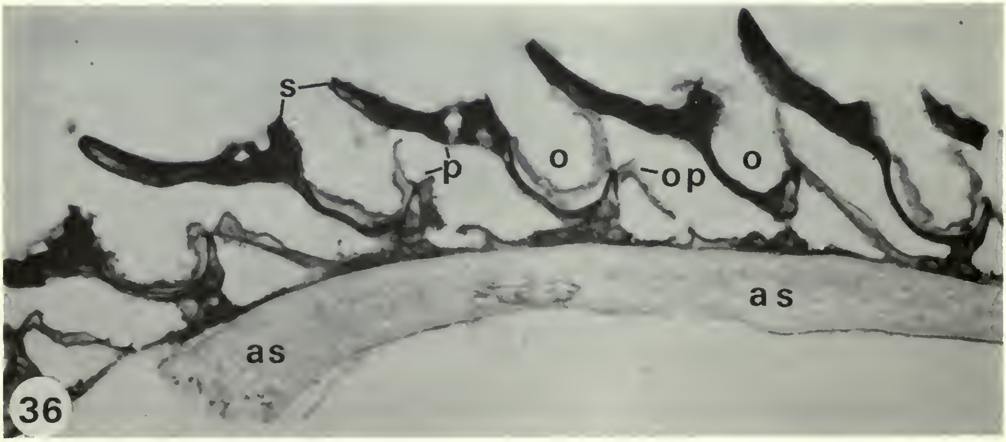
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Figs 34–36 Micrographs of longitudinal thin-sections of epoxy resin embedded specimens of Euthyrisellidae and Didymosellidae: (34) *Pleurotoichus clathratus* (Harmer) BMNH 1976.1.2.1, Queensland, showing large subfrontal hypostegal coeloms ×60; (35) *Euthyrisell obtecta* (Hincks) BMNH 1890.7.23.38, Torres Straits, visceral-to-hypostegal communication (arrowed) and minute subfrontal hypostegal coelom ×170; (36) *Didymosella larvalis* (MacGillivray) BMNH 1890.4.17.1–10pt., Spencer Gulf, zooids with cuticular basal walls encrusting algae ×40. *a* ascus, *o* ovicell, *op* operculum, *f* frontal process, *p* primary orifice, *s* secondary orifice, *h* hypostegal coelom, *sf* subfrontal hypostegal coelom, *v* visceral coelom, *b* basal coelom, *as* algal substratum.

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Ailsa M. Clark

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Notes on Atlantic and other Asteroidea. 1. Family Benthopectinidae

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Synopsis

Various taxa of the family Benthopectinidae, mainly from the Atlantic, are reviewed. The genera *Pectinaster* and *Cheiraster* are redefined, *Pectinaster* being restored to Perrier's concept of 1894 by transfer of several nominal species without specialized papularia to *Cheiraster*, which is enlarged by inclusion in it of *Luidiaster* Studer as a subgenus. Two further subgenera of *Cheiraster* are described, *Barbadosaster* for *Cheiraster echinulatus* (Perrier) and *Christopheraster* for *C. mirabilis* (Perrier), also including *C. blakei* sp. nov. and two other species. On the basis of older collections and new material, mainly from the *Pillsbury* and *Gerda* collections of the University of Miami, the morphological and geographical ranges of certain species of these two genera and of *Benthopecten* are extended and several names are put in synonymy, tabular keys to the Atlantic species are also included.

Introduction

In the course of a major review of the Atlantic species of Asteroidea, assessment of the neglected deep-sea family Benthopectinidae proved so complicated as to necessitate a preliminary paper to dispose of some of the more complicated taxonomic problems.

The ordinal position of the Benthopectinidae will be discussed in the main study on Atlantic asteroids (Clark & Downey). The family was removed from the Paxillosida to the revived order Notomyotida Ludwig, 1910 by McKnight (1975).

Systematic discussion

Family **BENTHOPECTINIDAE** Verrill, 1894

Archasteridae Benthopectininae Verrill, 1894 : 245–246, 268.
Archasteridae Pontasterinae Verrill, 1894 : 246–247, 268.
Benthopectinidae Verrill, 1899 : 200, 217; Ludwig, 1910 : 442, 458–461; Fisher, 1911 : 120–122; Verrill, 1914 : 310–311; Spencer & Wright, 1966 : U48.
Plutonasteridae Pontasterinae Verrill, 1899 : 200.
Cheirasteridae Ludwig, 1910 : 442, 444–447.

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Name	Range	Conclusions
Acontiaster bandanus Döderlein, 1921	East Indies, 304 m.	
Benthopecten Verrill, 1884		
B. acanthonotus Fisher, 1905	California, 1800–1940 m.	
B. chardyi Sibuet, 1975	SE Atlantic, 2580 m.	Subsp. of *B. simplex* (Perr.)
B. claviger Fisher, 1910	Bering Sea—Oregon, 1800–1950 m.	
B. cognatus Ludwig, 1905	Gulf of Panama, 3030 m.	
B. fischeri (Perrier, 1894)	NW Africa, 1060–1430 m.	
B. folini (Perrier, 1885)	NW Africa, 2320–2330 m.	Dates only from 1894
B. heteracanthus Macan, 1938	Gulf of Aden, 2310 m.	
B. huddlestoni (Alcock, 1893)	Bay of Bengal, 2780 m.	
B. incertus Ludwig, 1910	'Indian Ocean'	
B. indicus (Koehler, 1909)	S of Sri Lanka, 830–1080 m.	
B. moluccanus Fisher, 1913	East Indies, 760 m.	
B. munidae H. E. S. Clark, 1969	S New Zealand, 740 m.	
B. mutabilis Fisher, 1910	British Columbia, 2870 m.	?To *Gaussaster*
B. pectinifer (Ludwig, 1905)	Galapagos—California, 1570–2320 m.	
B. pedicifer (Sladen, 1889)	Southern Ocean, 2930–3480 m.	
B. pentacanthus Fell, 1958	New Zealand, 730 m.	
B. pikei H. E. S. Clark, 1969	New Zealand, 550–630 m.	
B. pikei var. *australis* H.E.S.C., 1970	New Zealand, 1650–1690 m.	
B. polyctenius Fisher, 1913	East Indies, 1470 m.	
B. rhopalophorus Djakonov, 1950	Okhotsk Sea, 420 m.	
B. semisquamatus (Sladen, 1889)	Japan, 1030–3430 m.	See p. 95
B. semisquamatus celebensis Döderlein, 1921	East Indies, 920–1890 m.	
B. simplex (Perrier, 1881)	North Atlantic, 2000–2740 m.	
B. spinosissimus (Sladen, 1889)	Ascension I., 780 m.	
B. spinosus Verrill, 1884	E of U.S.A., 1300–3700 m.	
B. spinuliger (Ludwig, 1905)	Galapagos—Panama, 1620–2320 m.	
B. styracius Fisher, 1913	Philippines, 1650 m.	
B. violaceus (Alcock, 1893)	Laccadive Sea, 2190 m.	
Cheiraster Studer, 1883		
C. coronatus (Perrier, 1884)	West Indies, 340–380 m.	Syn. of *C. mirabilis*
C. diomedeae Fisher, 1917	Philippines, 770 m.	
C. echinulatus (Perrier, 1875)	West Indies, 100–300 m.	To subgen. *Barbadosaster* nov.
C. enoplus Verrill, 1915	West Indies, 750–840 m.	Syn. of *C. mirabilis*
C. gazellae Studer, 1883	Philippines—East Indies, 360–470 m.	
C. granulatus Ludwig, 1910	'Indian Ocean'	
C. inops Fisher, 1906	Hawaiian Is—Sri Lanka, 430–1250 m.	

C. ludwigi Fisher, 1913	East Indies, 1270 m.	
C. mirabilis (Perrier, 1881)	West Indies, 300–900 m.	To subgen. *Christopheraster* nov.
C. monopedicellaris McKnight, 1973	New Zealand, 720–770 m.	
C. niasicus Ludwig, 1910	Philippines, East Indies, 490–930 m.	
C. otagoensis McKnight, 1973	New Zealand, 720–1090 m.	
C. pedicellaris Studer, 1883	NE Australia, 1000 m.	
C. pilosus (Alcock, 1893)	S India, 1080–1310 m.	
C. richardsoni Fell, 1958	New Zealand, 730 m.	
C. snyderi Fisher, 1906	Hawaiian Is—Nicobar Is, 420–1670 m.	
C. subtuberculatus (Sladen, 1889)	SE Australia, 1740 m.	
C. triplacanthus Fisher, 1913	East Indies—SE Africa, 1050–1280 m.	
C. trullipes (Sladen, 1889)	Philippines, 1920 m.	
C. weberi Döderlein, 1921	East Indies, 470 m.	
C. yodomiensis Goto, 1914	Japan, 160 m.	?To *Nearchaster*
Gaussaster antarcticus (Sladen, 1889)	Southern Ocean, 2730–3060 m.	
Luidiaster Studer, 1884		Subgen. of *Cheiraster*
L. antarcticus (Koehler, 1907)	Southern Ocean, 3250 m.	
L. dawsoni (Verrill, 1880)	Bering Sea—W Canada, 100–290 m.	
L. dubius H. L. Clark, 1941	West Indies, 485 m.	Syn. of *Cheiraster sepitus*
L. gerlachei (Ludwig, 1903)	Southern Ocean, 160–810 m.	
L. hirsutus Studer, 1884	Southern Ocean, South Africa, 240–550 m.	
L. horridus (Fisher, 1906)	Hawaiian Is, 260–330 m.	To *Cheiraster (Christopheraster)*
L. oxyacanthus (Sladen, 1889)	Japan, 630 m.	To *Cheiraster (Christopheraster)*
L. planeta (Sladen, 1889)	S Chile—Falklands & Argentina, 350–500 m.	
L. teres (Sladen, 1889)	East Indies, 260 m.	
L. tuberculatus Djakonov, 1929	Japan Sea, 140–850 m.	
Myonotus intermedius (Fisher, 1910)	California, 1380–1750 m.	
Nearchaster Fisher, 1911		
N. aciculosus (Fisher, 1910)	Alaska—California, 550–1460 m.	
N. fisheri Döderlein, 1921	East Indies, 830–1020 m.	
N. pedicellaris (Fisher, 1910)	Alaska, 510 m.	
N. variabilis (Fisher, 1910)	Bering Sea—Alaska, 200–640 m.	
N. variabilis geminus Djakonov, 1950	Okhotsk Sea, 500–520 m.	
Pectinaster Perrier, 1885		
P. agassizi (Ludwig, 1905)	Galapagos—California and Gulf of Aden, 790–2320 m.	
P. agassizi evoplus (Fisher, 1910)	S California, 1800–1940 m.	
P. agassizi granuliferus Macan, 1938	Gulf of Aden, 2000 m.	
P. cribellum (Alcock, 1893)	Laccadive Sea, 2190 m.	to *Cheiraster*
P. dispar Verrill, 1915	West Indies	
P. filholi Perrier, 1885	NW Africa—NE America, 1200–3100 m.	

Name	Range	Conclusions
P. gracilis Verrill, 1915	West Indies, 130–550 m.	Syn. of *Cheiraster planus*
P. hispidus (Alcock & Wood-Mason, 1891)	Arabian Sea—Laccadive Sea, 880–2470 m.	Syn. of *P. mimicus*
P. mimicus (Sladen, 1889)	Laccadive Sea—New Zealand, 690–1690 m.	
P. mimicus hylacanthus Fisher, 1913	Philippines—East Indies, 700–800 m.	
P. mimicus malayanus Döderlein, 1921	East Indies, 1020–1910 m.	
P. mimicus palawanensis Fisher, 1919	Philippines, 1330 m.	
P. mixtus Verrill, 1915	West Indies, 130–1830 m.	Syn. of *C. echinulatus*
P. oligoporus (Perrier, 1894)	West Indies, 275 m.	Syn. of *C. echinulatus*
P. pristinus (Sladen, 1889)	Uruguay, 4840 m.	Syn. of *P. filholi*
P. robustus A. H. Clark, 1917	Chile, 2410 m.	to *C. (Luidiaster)*
P. vincenti (Perrier, 1894)	West Indies, 170 m.	Syn. of *C. echinulatus*
Pontaster Sladen, 1885		
P. sepitus (Verrill, 1885)	NE America, 670–1570 m.	to *Cheiraster*
P. tenuispinus (Düben & Koren, 1846)	Arctic—C. Cod, Bay of Biscay, 20–2000 m.	
Saraster insignis A. H. Clark, 1916	Lower California, 840 m.	Syn. of *Nearchaster insignis*

This family of primarily deep-water Asteroidea is in need of review, the last comprehensive survey being by Ludwig (1910), intended only as a preliminary treatment, modified by Fisher (1911), while Macan (1938) simply listed the species of *Pectinaster* and *Benthopecten* (the genera represented in the Murray Expedition collections), summarizing earlier conclusions about these two genera.

Since the present study concentrates on the Atlantic fauna, the genera *Acontiaster, Myonotus* and *Nearchaster*—known only from the Indo-Pacific—have not merited attention here but are listed below with the other taxa currently recognized together with nomenclatural modifications now proposed. *Saraster* A. H. Clark, 1916, type and only species, *S. insignis* A. H. Clark, is now synonymized with *Nearchaster.* It was described without comparative remarks or figures and the holotype (from Lower California) has disintegrated but the description leaves no doubt in my mind that it was conspecific with *N. aciculosus* (Fisher, 1910), taken at 14 *Albatross* stations off California (and further north), any differences being accountable to the smaller size of the type.

Additionally, the following names formerly reduced to synonyms are now otherwise disposed:

Benthopecten armatus (Sladen, 1889), NE America—Portugal, 2290–2470 m., synonymized with *B. spinosus* Verrill by Macan, 1938, following Verrill, 1899 and Grieg, 1921, treated as valid by Farran, 1913 and Mortensen, 1927 but now synonymized with *B. simplex* (Perrier), following Ludwig, 1910.

B. fischeri Perrier, 1894. NW Africa, 1060–1430 m, synonymized with *B. spinosus* by Macan, 1938, following Grieg, 1921, but now provisionally treated as valid or a possible synonym of *B. simplex.*

Cheiraster planus Verrill, 1915, West Indies (no details), synonymized with *C. mirabilis* (Perrier) by Downey, 1973, but now considered as valid.

Pontaster perplexus Perrier, 1894, NW Africa, 2320–2330 m., synonymized with *P. tenuispinus* (Düben & Koren) by Ludwig, 1910, but now synonymized with *Pontaster sepitus* Verrill, which is itself now revived from the synonymy of (*C.*) *echinulatus* (Perrier), to which it was referred by Ludwig, 1910, and newly referred to *Cheiraster.*

Pontaster venustus Sladen, 1889, Azores—Portugal, 1250–4000 m., with var. *robusta* Sladen, 1889, Cape Verde Is area, depth ?, synonymized with *Pectinaster filholi* Perrier by Macan, 1938, following Ludwig, 1910, but now synonymized with *Cheiraster sepitus.*

B. semisquamatus (Sladen, 1889) was treated by Goto, 1914, without explanation as a synonym of *B. spinosus* Verrill, apparently extending Verrill's synonymy of *B. semisquamatus* var. *occidentalis* to the Pacific *semisquamatus* itself, despite Ludwig's retention in 1910 of this as valid, followed by Fisher (1919 : 210) and Döderlein (1921). Okutani (1969) has followed Goto.

The genera of Benthopectinidae can be distinguished by the tabular key (Table 1).

Some of the generic limits within the Benthopectinidae are still ill-defined. In Ludwig's review (1910), on the strength of the unusual dorsal arm muscles, the present family was interpreted as a suborder Notomyota including two families: Cheirasteridae (for *Cheiraster* Studer, 1883, *Luidiaster* Studer, 1884, *Pontaster* Sladen, 1885 restricted, *Pectinaster* Perrier, 1885, *Marcelaster* Koehler, 1907 and *Gaussaster* nov., of which *Marcelaster* was synonymized with *Luidiaster* by Fisher, 1940) and Benthopectinidae (for *Benthopecten* Verrill, 1884 and *Pararchaster* Sladen, 1885). The latter group was distinguished by the presence of odd interradial marginal plates, the superomarginal ones with unusually large spines.

Fisher (1911) described two new genera, *Nearchaster* and *Myonotus*, both with the

Table 1 Tabular key to the genera of Benthopectinidae. Entries in brackets indicate a slight development or tendency.

	1	2	3	4	5	6	7	8	9
Benthopecten	A	w/b	L	f	M/R	+	2 (3)	p	F
Myonotus	A	w/b	L	p	M	+	2	p	F
Nearchaster	I	w	L	p	M	+	2 (3)	p	F
Gaussaster	I	b	L	f	R (M)	+	3,2	p	F
Acontiaster	R	w	D	p	M	(+)	2	u	F
Cheiraster (*Luidiaster*)	R	b (w)	L	p	M	−(+)	2	p	F
Cheiraster (*Barbadosaster*)	R	b	D	f (p)	M	−	2 (3)	p	F
Cheiraster (*Christopheraster*)	R	d	D	p (f)	M	+	1 (2)	p	F
Cheiraster (*Cheiraster*)	R	b	D	p	M	−	1	p	F
Pectinaster	R	o	L	p	M/R	−	1	p	F
Pontaster	R	o	L (D)	p	M	−	2,3	p	B

1. Interradial suture between the marginal plates:
   A–absent, an odd plate present in each series, the superomarginal one inset on to the disc
   I–often irregular, plates asymmetric or odd plates in some or all interradii but the superomarginal one on the periphery of the disc
   R–regular, no odd interradial plates (though the sutures are occasionally asymmetric in one or two interradii)

2. Papular areas:
   b–bilobed distally (except in small specimens, R <30 mm), limited to the arm bases, initiated from a single median proximal primary pore
   d–initially double, two lateral areas on each arm base merging proximally in large specimens, R >80 mm, to form a bilobed area, pores relatively small and interstitial
   o–oval and swollen with deepened plates forming well-defined median papularia
   w–widespread over most of disc and at least the proximal parts of the arms

3. Superomarginal plate alignment:
   D–partly or mainly dorsal, framing the paxillar area in dorsal view
   L–mainly lateral, inconspicuous dorsally

4. Abactinal plates of disc and arm bases:
   f–flat, usually scale like, with only a small median elevation, if anything
   p–(para-)paxilliform with a more or less well defined median column or convexity

5. Armament of most abactinal plates:
   M–multiple, with a cluster of spinules, often surrounding a larger median spinelet or spine, sometimes totally lacking
   R–reduced, often to a single spinule or spinelet throughout

6. Central armament of primary and some other proximal plates
   +–large spines 2+ mm long present
   −–only 1 (rarely 2,3) central spinelets of larger plates enlarged up to *c.* 1·5 mm

7. Subambulacral spine number

8. Dorsal arm muscles:
   p–paired, attached proximally to one or two ambulacral plates and the adjacent marginals, or to the abactinal body wall, or both
   u–united in a single mass, attached proximally only to the body wall

9. Pedicellariae (if present):
   B–bivalved with only two elongated valves, on adambulacral plates only
   F–fasciculate with multiple narrow tapering valves, usually in two, occasionally three, combs on adjacent plates (pectinate), usually present on actinal plates, sometimes on abactinal and marginal plates, occasionally lacking.

interradial marginals more or less irregular in position, so that one plate of each series is often more or less mid-interradial but the armament of such odd superomarginals is not conspicuous. Inevitably, such intermediate taxa prompted him to amalgamate the Cheirasteridae with the Benthopectinidae. Apart from synonymizing *Pararchaster* with *Benthopecten,* he accepted the genera cited by Ludwig.

Among the genera with no odd interradial marginals, Fisher distinguished *Pontaster* and *Pectinaster* with 'entire and swollen' papularia from *Cheiraster* and *Luidiaster* with 'flat and two-lobed' papular areas, separating *Pontaster* from *Pectinaster* on the presence of bivalved rather than fasciculate pedicellariae and *Cheiraster* from *Luidiaster* on the single rather than multiple subambulacral spines—the only difference evident from a comparison of Ludwig's diagnoses. To supplement these criteria, Fisher proposed to use the proximal attachment of the dorsal arm muscles—to one or two ambulacral plates and the two adjacent marginals in *Luidiaster* but to the dorsal body wall and the superomarginals in *Cheiraster.* However, in 1919 he had to modify this after finding that the type-species of *Cheiraster, C. gazellae* Studer, does have tendons to the twelfth and thirteenth ambulacral plates, though inconspicuous ones, and these plates lack the enlarged crests of the comparable plates of *L. hirsutus,* the type species of *Luidiaster*, and even more *L. dawsoni.* I find that *L. hirsutus* additionally has the attenuated proximal ends of the muscles attached to the dorsal body wall just distal to the V-shaped area defined by the two lobes of the papular area, as well as having a tendon to a laterally swollen crest of an ambulacral plate (the sixth plate in a specimen with R 85 mm). Fisher himself (1940) found a much stouter link between the main part of the muscle and the dorsal body wall in the *Discovery* specimen of *Pontaster planeta* Sladen, a species later referred to *Luidiaster* (A.M.C., 1962) on account of the V-shaped flat papular areas and multiple subambulacral spines, and closely related to *L. hirsutus.* The muscle appears to me to extend nearly to the seventh ambulacral, ending opposite the fourth superomarginal, the distalmost papular pores being just proximal to this (as in *L. hirsutus*), although Fisher described it as ending level with the ninth ambulacral. He also noted a 'rudimentary' tendon to the eighth ambulacral in *planeta.* In *Cheiraster mirabilis* (Perrier), which has abruptly enlarged fourth superomarginal plates, I find that there is a stout tendon to this marginal and the adjoining seventh ambulacral but no connection to the dorsal body wall.

Clearly, the muscle attachment shows too great a range in these various species for use as a character of generic weight. This leaves only the number of subambulacral spines to distinguish between *Cheiraster* and *Luidiaster* but I think that the alignment of the superomarginal plates is also of more than specific significance. Hitherto, this alignment has not been regarded as important, possibly because of the considerable range of form in the very variable species *Pontaster tenuispinus*, so that Ludwig suggested synonymy of *Pontaster venustus* with dorsally broad superomarginals with *Pectinaster filholi* where the marginals are almost entirely lateral. However, limitation of *Pectinaster* to species with laterally aligned superomarginals results in a much more natural grouping, since such species also have specialized compact papularia, those with dorsally broad superomarginals having much more diffuse pore areas potentially or actually bilobed in form with the abactinal plates within the areas little modified (compare Figs 1a & b). Verrill (1915 : 137) discounts the importance of the subambulacral spine number in ascribing the specimen he named *enoplus* to *Cheiraster* despite the two large subambulacral spines of the large holotype (R 185 mm). Study of a good size range of *C. mirabilis* now shows that doubling of the subambulacral spine number is common in very large specimens, R >120 mm, and that *C. enoplus* Verrill is a synonym, the holotype sharing the very distinctive abrupt enlargement of the fourth superomarginal plates and spines.

With regard to the Atlantic species of Benthopectinidae, no less than 18 other nominal species which have been included in *Pontaster, Pectinaster, Cheiraster* and *Luidiaster* need to be taken into consideration, namely (in chronological order):

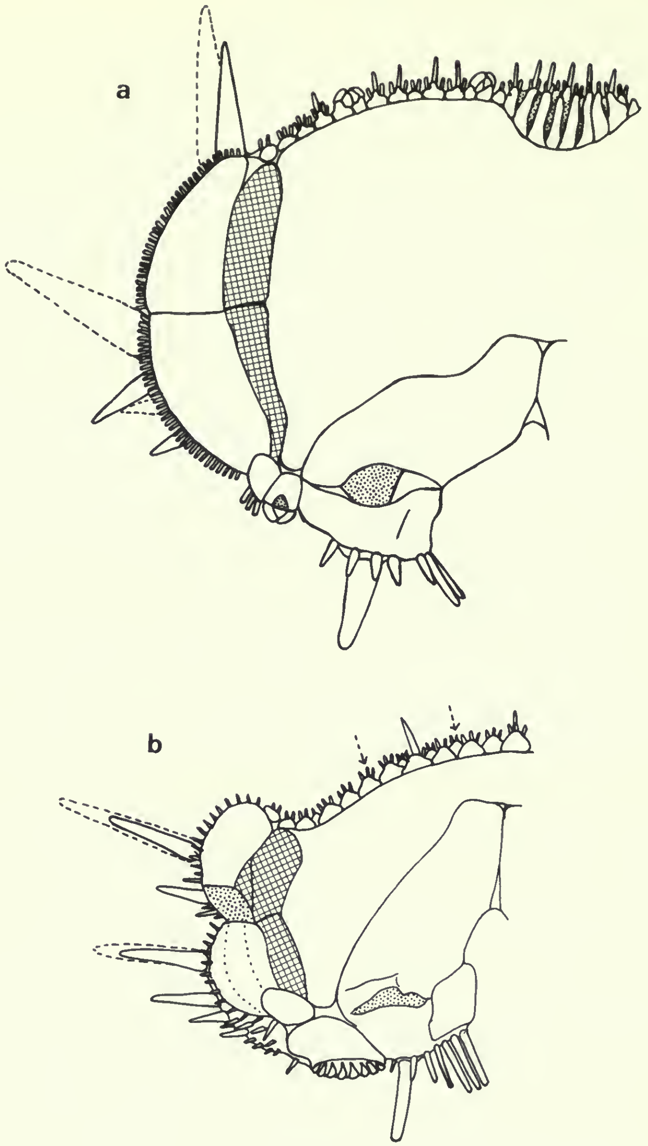


Fig. 1 Half sections through the base of a ray bisecting the papularium or papular area, showing the armament of the second supero- and inferomarginal plates with their proximal and internal (hatched) faces, the fully developed spines of the third plates shown by discontinuous lines. (a) *Pectinaster filholi* Perrier, syntype of *Pontaster forcipatus* Sladen, *Challenger* st. 44, 45 or 50, BMNH no. 90.5.7.50(pt), R *c*.75 mm; (b) *Cheiraster (Christopheraster) blakei* sp. nov. *Oregon* st. 4294. R. *c*. 70 mm. [In (b) the vertical faces of the two marginals are not in the same plane; the position of the lobe of the papular area is indicated by the arrows.]

Pontaster tenuispinus (Düben & Koren, 1846)	NE Atlantic, Arctic
Cheiraster echinulatus (Perrier, 1875)	West Indies
C. mirabilis (Perrier, 1881)	West Indies
Luidiaster hirsutus Studer, 1883	Kerguelen, South Africa
C. coronatus (Perrier, 1884)	West Indies
Pontaster sepitus (Verrill, 1885)	NW Atlantic
Pectinaster filholi Perrier, 1885	NE Atlantic
Pontaster venustus Sladen, 1889	Azores, Cape Verde area
Pectinaster pristinus (Sladen, 1889)	SW Atlantic
Luidiaster planeta (Sladen, 1889)	E & W Patagonia, Falklands
Pectinaster vincenti (Perrier, 1894)	West Indies
Pontaster perplexus Perrier, 1894	West Indies
Pectinaster oligoporus (Perrier, 1894)	West Indies
P. dispar Verrill, 1915	West Indies
P. gracilis Verrill, 1915	West Indies
P. mixtus Verrill, 1915	West Indies
C. planus Verrill, 1915	West Indies
Luidiaster dubius H. L. Clark, 1941	West Indies

Of these, *Pontaster venustus* was synonymized with *Pectinaster filholi* by Ludwig (1910), followed by Macan (1938) but is now found to be referable to *Cheiraster* because of its irregular bilobed papular areas and dorsally broad superomarginal plates. The oval, well-defined papularia of *P. filholi* are constructed of much deeper plates than the other abactinal ones, laterally grooved to accommodate the papulae (Fig. 1a). The same combination of less compact actually or potentially bilobed papular areas and relatively broad superomarginals as in *P. venustus* is also shown by the types of *Pontaster sepitus, Pectinaster vincenti, Pontaster perplexus, Pectinaster oligoporus, Pectinaster dispar, Pectinaster gracilis* and *Pectinaster mixtus,* all of which have been examined. These encompass a size range of R 26–*c.* 55 mm.

Pectinaster pristinus is known only from a single small specimen, R *c.* 18 mm, from off the River Plate. This was in poor condition, the abactinal plates obscured by mud; when this was removed, no significant difference could be seen in the armament from specimens of *P. filholi* of similar small size from the North Atlantic.

Accordingly, both *Pontaster* and *Pectinaster* are reduced in the Atlantic to single species (indeed *Pontaster* is a monotypic genus).

Following study of many benthopectinids from the U.S. National Museum and M.C.Z., Harvard collections, together with the *Pillsbury* and *Gerda* material of the University of Miami from the tropical Atlantic, I consider that most of the 16 remaining names listed above (which fall within the scope of *Cheiraster* and *Luidiaster*) are synonyms, only five being for valid species. This superfluity of names arose mainly from Perrier's confused treatment of the *Blake* collections (1881 and 1884 with afterthoughts in 1894), which was partly resolved but further complicated by Verrill's failure to take growth changes into account in his review of 1915.

One character of limited use is the R/r ratio, which tends to increase with the absolute size, so that species such as *C. mirabilis,* which may exceed R 120 mm, may achieve an R/r ratio of as high as 9/1, from usually 7–8/1 at R *c.* 100 mm or only *c.* 5/1 at R 20 mm. However, in *C. sepitus* with a maximum R of probably 70 mm, the ratio stays near 5/1 in specimens larger than R *c.* 30 mm.

Since individual papulae do not appear to increase disproportionately in size with growth of the whole animal, their number must increase in order to maintain adequate respiratory function. In most of the species under discussion the first (primary) pore usually appears at R 10–15 mm near the base of each arm distal to the primary radial plate, which at this small size is usually still distinguishable among the other disc plates; further pores, usually smaller, are added progressively around it, especially distally and laterally. Only *Cheiraster mirabilis* and *C. coronatus* (sensu H. L. Clark, 1941) differ from the rest in developing not one primary

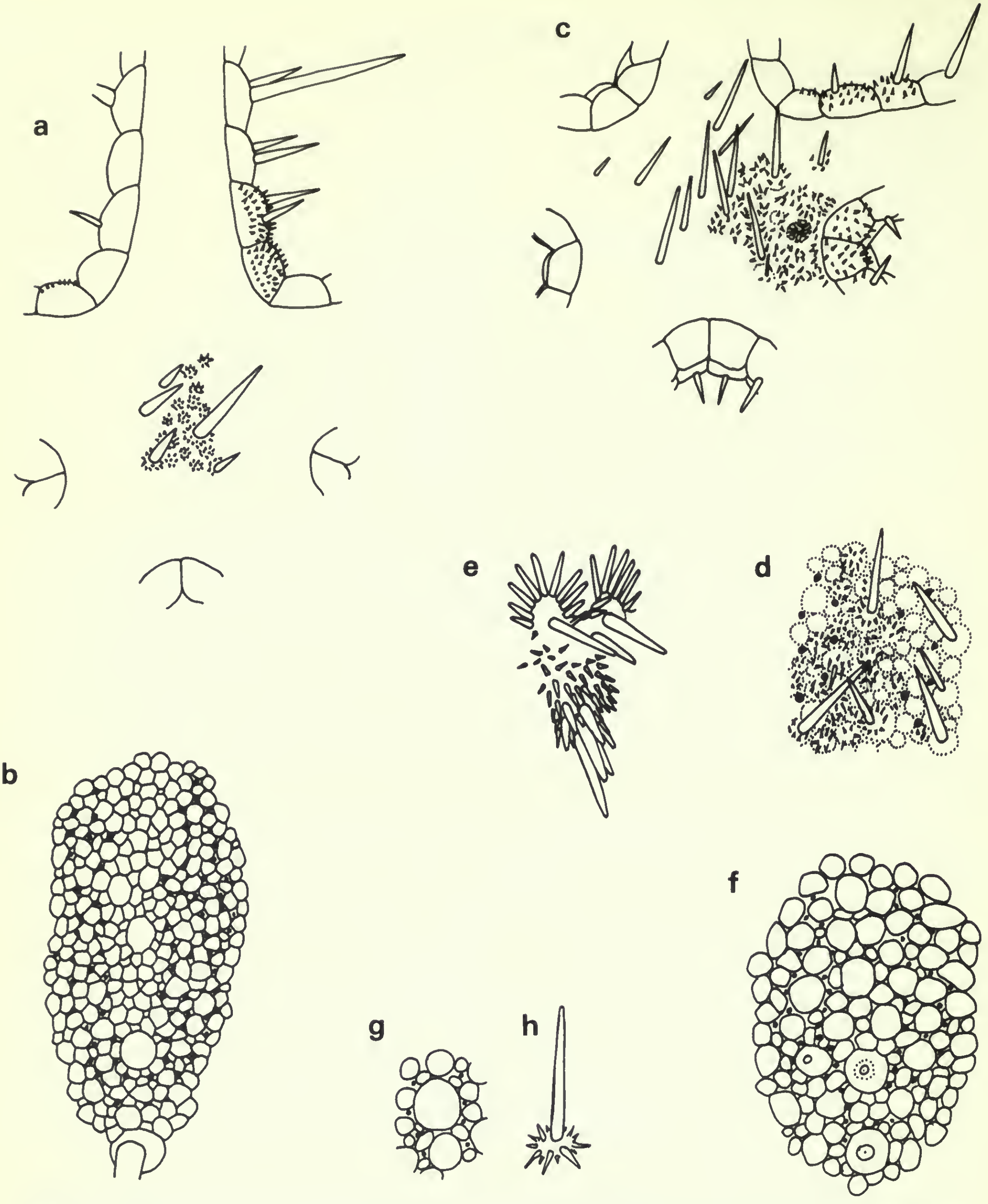
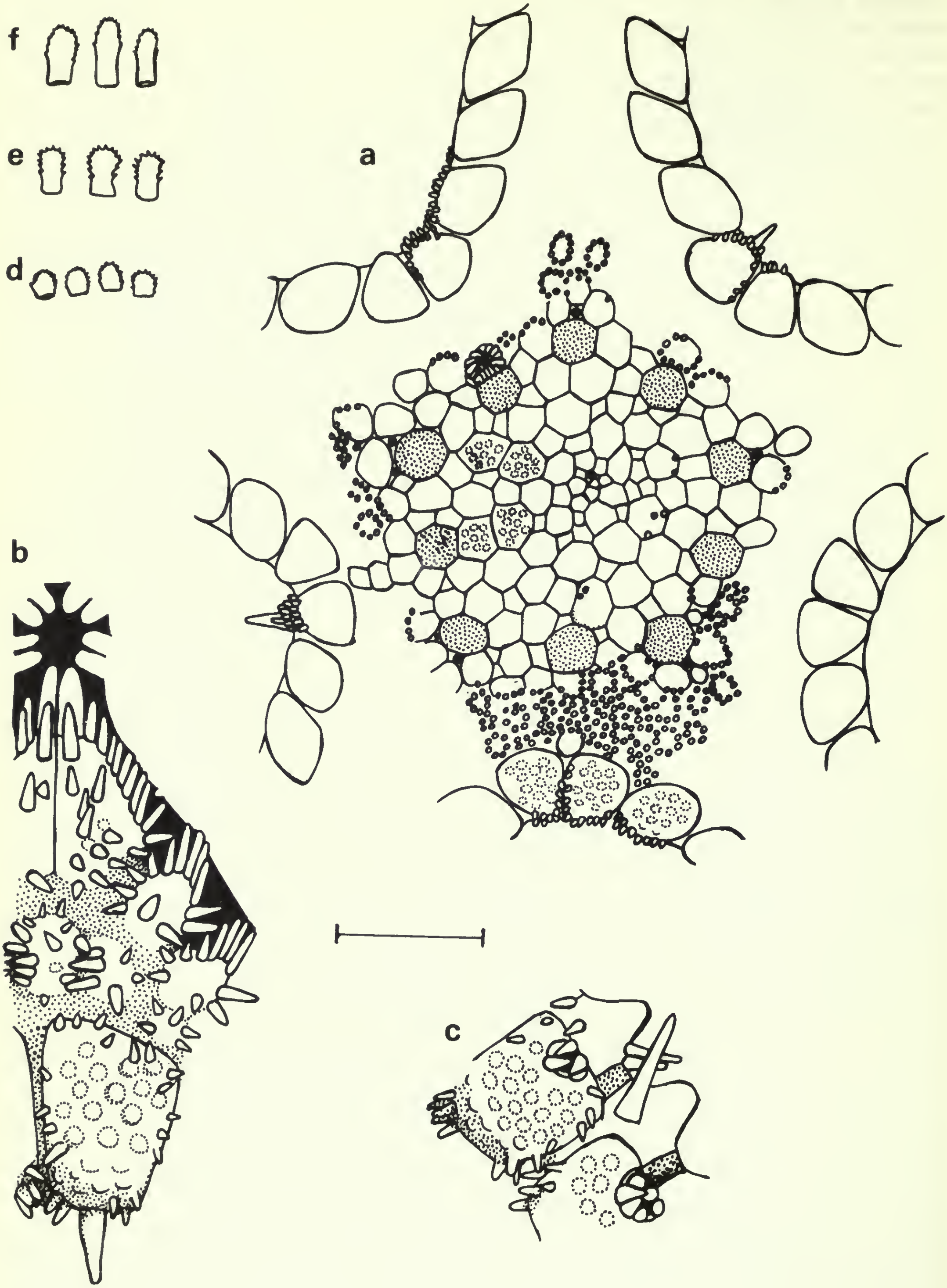


Fig. 2 (a and b) *Cheiraster (Christopheraster) mirabilis* (Perrier). (a) *Atlantis* st. 3444, 3445, 3447 or 3449, MCZ 3912(pt), R 25 mm, to show disc and proximal marginal spines; (b) Holotype, *Blake* st. 148, MCZ 10, R 87 mm, papular area (the proximal end lowermost); (c–f) *Cheiraster (Christopheraster) blakei* sp. nov. (c) *Atlantis* st. 3444, 3445, 3447 or 3449, MCZ 3912(pt), R 21 mm, for comparison with (a); (d) *Atlantis* st. 2963F, MCZ 3915, R 112 mm, part of intact papular area (most of the spines unnaturally appressed); (e) *Blake* st. 19, MCZ 2179, R *c.* 40 mm, second inferomarginal plate, adjoining actinal area and two adambulacral plates; (f) *Blake* st. 295, MCZ 216, R *c.* 45 mm, denuded papular area showing the spine sockets on two midradial plates, the upper one probably the primary radial; (g, h) *Cheiraster (Christopheraster) horridus* Fisher, holotype, *Albatross* st. 4079 (Hawaiian Is), USNM 21156, R 35 mm; (g) part of denuded papular area showing varied plate size and relatively small pores; (h) armanent of one large disc plate.

pore but a pair of smaller pores offset one each side of the primary radial plate; additional similarly small pores appear laterally and distally but few develop in the proximal mid-radial area, even at a large size, so that the two lateral pore areas only become loosely linked (Fig. 2b & f). At R >100 mm, the total pore number in these two species exceeds 100 on each ray, far more than in the other species of *Cheiraster* with their larger papulae, so that for instance *C. planus* at R 100 mm has only *c.* 50 pores in each area. From the median primary pore these develop fairly regularly in this species in a curved double row on each side, forming a horseshoe-shape; only at R >70 mm do the added pores form a more irregular and elongated area (Fig. 5). The early stages of this sequence are shown by the illustrated holotype and paratype of *Pectinaster gracilis* (Verrill, 1915, pl. 6, fig. 1 & pl. 15, fig. 1b); the smaller paratype (R probably *c.* 20 mm) has only three pores in a transverse line, the median one enlarged, while the holotype (pl. 6) at R 30 mm usually has just two additional pores placed distal to the lateral ones forming a very shallow U. Although not stated by Verrill, the holotype has most superomarginal spines distinctly longer and stouter than the corresponding inferomarginal spines—a characteristic of *C. planus*—as well as compact parapaxillae, uniformly short inferomarginal spinules giving a smooth contour to the plate (apart from the main and accessory spines), large single subambulacral spines and relatively blunt-angled furrow margins to the adambulacral plates. Consequently, *P. gracilis* should be treated as a synonym of *C. planus.*

A similar sequence in the early development of pores is shown in *Cheiraster echinulatus, Pectinaster vincenti* and *P. mixtus,* also in *Pontaster sepitus, P. venustus, P. perplexus, Pectinaster oligoporus* and *P. dispar* (and almost certainly occurred in the holotype and only recorded specimen of *Luidiaster dubius* before it reached its final size of R *c.* 60 mm). In these, however, the later developed pores are more irregular in position than those of *C. planus,* forming at first a square or transverse patch (Fig. 4b) and then an elongated bilobed area, often asymmetrically so or with the distal pores of the two lobes approximating medially (as in the holotype of *P. vincenti,* Fig. 4g) to form an almost oval area. The maximum R in these nominal species does not appear to exceed 70 mm and the pore number 36. Most specimens taken are in the R 20–40 mm range. (Genital pores first appear in *Cheiraster* at R 10–15 mm close to the first superomarginal plates.)

The holotypes of *C. echinulatus, mixtus* and *vincenti* have R 16 mm, 26 mm and 42 mm and the pore number in each area is 1–3, 3–5 and *c.* 12 respectively, an increase compatible with the size differences. All show the following characters: the abactinal plates are very mixed in size, polygonal, abutting fairly closely together, distinctly flattened in the two smaller specimens but somewhat convex in the larger one, especially on the papular areas, armed with numerous (up to *c.* 30) short 'spinules' of superficially granuliform shape (though with height/breadth >2/1 in the largest) arising from most of the surface of the plate and encircling in a double ring on many plates a slender needle-like spinelet; the superomarginal plates are broad in dorsal view, the two opposite ones together taking up *c.* 50% of the total arm breadth; the marginal spines are relatively slender, most inferomarginal ones longer than the corresponding superomarginal spines, while several of the inferomarginal spinules below the spine are more or less enlarged into accessory spinelets so as to give a rough profile to the body; the furrow margins of the proximal adambulacral plates form an acute angle prolonged into the furrow (the distal plates being truncated) and the subambulacral spines are multiple (except perhaps in the small holotype of *C. echinulatus* where Perrier described a complete circle of 10–12 peripheral spines (including those projecting over the furrow, around a larger central spine but all the subambulacral spines are now [1980] lost or displaced). The coincidence of all these characters is convincing evidence that the three are conspecific, so that *Cheiraster vincenti* and *Pectinaster mixtus* become synonyms of *C. echinulatus.* The type localities of *C. echinulatus* and *vincenti* are near the neighbouring Lesser Antillean islands of Barbados and St Vincent; that of *mixtus* is off Havana, Cuba (Verrill's 'West of Florida' deriving from a misreading of the coordinates for *Albatross* st. 2341). Many other specimens from intermediate and western caribbean localities to a confirmed depth of 567 metres show variation not only in the convexity of the


f
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abactinal plates and arrangement of the pores but also in the size of the pores, which reach a maximum number of 36 in a specimen with R 65 mm. The frequency of pedicellariae, as usual, is rather variable; there are some pectinate actinal ones is *c.* 50% of specimens but only *c.* 5% (including the holotypes of *C. echinulatus* and *mixtus*) have a few fasciculate inferomarginal pedicellariae adjoining the adambulacrals. The holotype of *P. oligoporus* from the Leeward Is. in 275 m is in very poor condition but its flattened abactinal plates and the prolonged furrow angles of the adambulacrals show that it too is conspecific with and a synonym of *C. echinulatus.*

For the rest, the type localities of *C. sepitus, venustus* (with var. *robusta*), *perplexus, dispar* and *dubius* are scattered all over the North Atlantic, respectively: S of Cape Sable, Nova Scotia, 1570 metres, the Azores, 1650 metres (Cape Verde Islands, depth unknown), off Cap Blanc, W. Africa, *c.* 2325 metres, the Leeward Is, 1260 metres and S of Cuba, 485 metres. (For *Pectinaster dispar* Verrill cited the source as an *Albatross* station, locality unknown, but the labels now with the specimen indicate st. 2751, which is 16° 54′ N, 63° 12′ W.) The relevant type specimens have R measurements and pore numbers as shown in table 2.

Table 2

Name	*sepitus*	*venustus*	v. *robusta*	*perplexus*	*dispar*	*dubius*
R (mm)	37	37	46	52	35 + (?45–50)	*c.* 63
Pores	15	7–9	8	21	10–13	11–14

The figures for C. sepitus are from what may be called a ‘topotype’ in the USNM, no. 24525, since the two syntypes (from *Albatross* st. 2072) are now in a state of disintegration and were never properly described by Verrill. This specimen was named *P. sepitus* in Verrill’s hand and was from a station (2075) with almost identical coordinates and depth.

Although sharing with *C. echinulatus* the dorsally broad superomarginal plates taking up 50% or more of the arm breadth, these all differ from that species in several features. The abactinal plates are more loosely joined and consistently markedly convex and parapaxilliform, with more elongate and somewhat pointed spinules usually numbering only 5–15, clustered together on the central (highest) part of the plate, though again often surrounding a central spinelet several times longer; the superomarginal plates, though with a similar mean breadth to those of *C. echinulatus,* are somewhat longer and often more convex, numbering only *c.* 16 at R 20 mm or *c.* 27 at R 50 mm, compared with *c.* 20 and *c.* 30 at the same sizes in *echinulatus*; the marginal spines are shorter and much stouter basally, being conical in shape, though again the inferomarginal spines tend to be longer than the superomarginal ones and the upper inferomarginal spinules are likewise more or less elongated; the subambulacral spines are usually single, stout-based and conical (as usual in all these species similar in form to the marginal spines) and pedicellariae are rarely present at all, even on the actinal plates they were only found in less than 10% of specimens. Possibly in larger specimens, R > 50 mm, the arms remain relatively shorter than in *C. echinulatus*, R/r not much exceeding 5·0/1 where *echinulatus* may reach 6/1, but this remains to be seen from

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Fig. 3 *Cheiraster (Barbadosaster) echinulatus* (Perrier) (a) Holotype, *Hassler,* Barbados, Paris Museum (PM) 3481, R 16 mm, disc and arm bases from above, the primary radial and interradial plates stippled, crystal bodies indicated on a few larger abactinal and marginal plates (the centre of the disc rubbed almost bare of spinules); (b, c) the same, part of a ventral interradius and the fourth and fifth adambulacrals with adjacent inferomarginal plates, most armament lost, the subambulacral spine drawn on the fifth plate appressed; (d–f) abactinal spinules of: (d) the holotype of *C. echinulatus,* (e) holotype of *Pectinaster mixtus* Verrill, R 26 mm and (f) specimen from *Gerda* st. 628, R 66 mm. The scale equals 2 mm for (a), 1 mm for (b) and (c) and *c.* 0·5 mm for (d)–(f).

further intact specimens. (Perrier's implication that there is more than one subambulacral spine in the holotype of *perplexus* is not borne out by re-examination. It may also be noted that he gave the pore number as 'une quinzaine' but removal of the spinelets in one area revealed the higher number of 21. Verrill's estimate for the type of *dispar* was also too low).

With all these features in common, I do not think that the wide spread of pore numbers from 21 at R 52 in the type of *perplexus* to only 8 in that of the geographically close *venustus* var. *robusta* at R 46 mm is significant. The 'topotype' of *sepitus* has as many as 15 at R <40 mm. Other similar specimens, with R 19–46 mm collected at five *Pillsbury* stations off Venezuela and two *Discovery* ones from the Azores, all of which I consider are conspecific with *C. sepitus*, have 0–12 pores in individual areas, often with a range of three or more in different radii of the same specimen, one with R 41 mm, having from 6 to 12 pores in the five radii. Consequently, *P. venustus, perplexus, dispar* and *L. dubius* are now referred to the synonymy of *C. sepitus*, the oldest name.

All the West Indian *Pillsbury* specimens now referred to *C. sepitus* are from depths greater than 1000 metres, as with the type locality of *P. dispar*, which casts doubt on the depth record of only 485 metres for the holotype of *L. dubius*.

A further nomenclatural problem remains to be resolved concerning the two species generally known as *C. mirabilis* and *C. coronatus*, at least sensu H. L. Clark, 1941.

In his preliminary account of the *Blake* asteroids, Perrier (1881) described *Archaster mirabilis* (stations unspecified) firstly (paragraphs 1–4) from a specimen with R/r given as 87/12 mm, only 6–10 spines around the anus and otherwise granulous abactinal plates; he then commented on another specimen with R/r 45/12 mm. In the full report (1884) the first specimen is redescribed at the beginning of the account of *A. mirabilis*, the station given as 148, St Kitts, and the second specimen is separated off as holotype of *Archaster insignis* (since referred to *Dytaster* in the Astropectinidae), as noted by Verrill (1915). Other specimens from 46 different stations were also included under the name *mirabilis* but the one with R 87 mm from st. 148 must be the holotype.

Also in 1884, Perrier described *Archaster coronatus* from a specimen with R 65 mm, R/r 8/1, citing stations 2 and 19. The sample from st. 19 is in the MCZ, Harvard, labelled as syntypes but the largest specimen is badly broken and its R probably did not exceed 40 mm, so, as Verrill (1915) assumed, the holotype must be from st. 2, off Havana, Cuba, and in the Paris Museum. In 1894, Perrier inadmissably redescribed the holotype of *mirabilis* (R/r slightly modified to 85/10) as '*C. coronatus* premier type', as Verrill (1915) noted when he repeated Perrier's 1884 description for *coronatus*, ranking it as a subspecies of *mirabilis*. H. L. Clark (1941) satisfactorily distinguished two West Indian species of *Cheiraster* with spines several mm long on the disc in the following terms:

	mirabilis		*coronatus*
1.	Paxillae very low and closely covered by a group of minute spiniform granules, none of which are enlarged or lengthened into spinules [spinelets in my terminology.]	1.	Paxillae more convex with fewer and more unequal granules, one (or sometimes more) of them elongated into a spinule.
2.	3–10 relatively conspicuous spines 3–8 mm long at the centre of the disc.	2.	Spines up to 3–4 mm long but never forming a conspicuous isolated group.
3.	Fourth superomarginal spine up to 10–12 mm long.	3.	Fourth spine up to 5 mm long.

After examining the *Blake* and *Atlantis* specimens in the MCZ and the *Gerda* and *Pillsbury* material I can add the following:

1a.	Abactinal plates too low to be called 'paxilliform'; armed with up to *c.* 35 (mean number *c.* 15) short pointed spinules in compact groups.	1a.	Armament of abactinal plates consisting of up to *c.* 25 (mean *c.* 10) distinctly elongated radiating spinules, the longer central spinelets graduated to the disc spines.

2a.	The big disc spines closely clustered in the centre, not extending to the primary radial plate on the arm base; usually 5–15 spines, rarely >20.	2a.	Big spines spaced, extending on to the papular areas in larger specimens and graduating to the central paxillar spinelets, usually >10 even at R only 30 mm, up to *c.* 75 at R 100 mm.
3a.	Fourth (rarely the fifth) superomarginal plate and spine abruptly enlarged, the corresponding inferomarginal plate reduced and often spineless.	3a.	In larger specimens the fifth or sixth marginal spines the largest and graduated to the adjacent spines.
4.	Marginal plates covered with fairly uniform short pointed spinules, only a few on the lower face of the inferomarginals enlarged to spinelets; profile superficially smooth.	4.	Several more or less elongated spinules/spinelets at the upper end of the inferomarginals giving a shaggy appearance and rough profile.
5.	Furrow margins of adambulacral plates rounded or with obtuse angles.	5.	Furrow margins 90° or acute, angles prolonged into the furrow.

Unfortunately, Perrier's 1884 description of *C. coronatus* described the abactinal armament as including *c.* 15 spines *around the anus* and the fourth superomarginal spine as *much larger than the others* (my italics). Although 15 disc spines is a high number for *C. mirabilis* at R 65 mm it is not unprecedented (see Table 4). Accordingly, it seems unavoidable that the name *coronatus* should be referred to the synonymy of *mirabilis*, as was done by Downey (1973), following Ludwig (1910), though evidently without appreciation of the existence of the two species recognized by H. L. Clark.

A new name is therefore needed for the species with less conspicuous, more numerous and graduated disc spines and graduated superomarginal spines. Although H. L. Clark has the credit for distinguishing the species, knowing his antipathy to the use of personal names I propose the name *C. blakei* after the ship which first collected it. As the MCZ specimens from *Blake* station 19 are in poor condition, a large specimen from *Gerda* st. 918 (between Florida and the Bahamas), described on p. 113 has been selected as holotype.

Turning to the species of *Luidiaster* (other than *L. dubius* disposed of above), the smallest specimen available of *L. hirsutus* from South Africa has R *c.* 35 mm (R/r 4·5/1) and *c.* 30 pores/area but a primary median pore is distinguishable, as in *Cheiraster* sensu stricto. The pore areas are V-shaped with mostly two rows of pores in each limb whereas larger specimens, R *c.*80 mm, have 110–160 pores in a more irregular but still bilobed area. The type series of *L. planeta* from Chile, R 26–37 mm, shows 9–14 pores and the primary ones are distinct. These two southern species, *L. hirsutus* and *L. planeta,* both have the superomarginals inconspicuous in dorsal view, aligned mainly on the sides of the arms, unlike the species of *Cheiraster.* They also have two or more large subambulacral spines (though at R 35 mm in *L. hirsutus* the two spines are more or less markedly unequal) and H. L. Clark (1926) found single spines in his smallest specimen, R 16 mm). However, the West Indian *Cheiraster echinulatus* has two or even three subambulacral spines from a small size, R. *c.* 20 mm, while large specimens of *C. mirabilis* and *C. blakei* (R >100 mm) often develop a second spine, though most individuals have only one on most plates. (Second spines usually appear first on the distal half of the arm and on the very first plate.) Although large specimens of *C. mirabilis* and *blakei* may have the superomarginal plates relatively narrow dorsally, they still form a small border to the paxillar area and in *C. echinulatus* they are consistently broad.

I doubt whether the alignment of the superomarginal plates unsupported is of sufficient weight to justify a generic distinction for *Luidiaster hirsutus* so that *Luidiaster* is now treated as a subgenus of *Cheiraster.* Both names were introduced by Studer, 1883, who separated them, and even referred *Luidiaster* to the Astropectinidae, because the specimens of *Cheiraster gazellae* had the dorsal body wall sufficiently transparent to show the underlying muscles, which he took for gonads. However, he failed to name a type species for *Luidiaster* until 1884, from which date only the name is valid.

The main characters by which the seven Atlantic species of *Cheiraster* can be distinguished are summarized in Table 3. (The number of adambulacral plates corresponding to the first ten inferomarginals does not seem to me to be significant in *Cheiraster*, though it may be useful for certain species of *Benthopecten.*) Synonymies and ranges for five of these species are given on pp. 112–8.

Table 3 Tabular key to the Atlantic species of *Cheiraster* sensu lato. Brackets signify occasional or partial conditions.

	1	2	3	4	5	6	7	8	9	10	11	12
blakei	6·0–8·5/1	20/27/33	M	c	D	e	I	g	(R)	1 (2)	AM (D)	*c.* 130
mirabilis	7·5–8·5	20/30/37	L	(f)	D	a	I	u	R	1 (2)	AM (D)	185
hirsutus	5·5–7·0	20/27/*c.* 35	A	c	PC	e	I	g	(P)	2,3 (1)	(A)	92
planeta	*c.* 5	20/35/?42	A	c	PC	e	I	g	R,* P	2,3 (1,4)	(A,D)	100
planus	6·0–7·0	18/25/30	A	c	PC	e	S	u	R	1	A (M)	*c.* 100
sepitus	4·5–5·5	16/25/30	A	c	PB	e	I	g	(P)	1	((A))†	*c.* 60
echinulatus	4·8–6·0	19/27/34	A	f	PB	e	I	g	P	2 (1–3)	A (M)	*c.* 70

**C. planeta.* In the type series from S Chile, the furrow margins are acute but not in the Falkland Is specimen.
†*C. sepitus.* Only five out of 60+ specimens examined have any actinal pedicellariae.

1. R/r at R 50+ mm.
2. Number of superomarginal plates at R 20, 40 and 60 mm (some obtained by extrapolation)
3. Disc spines:
    L–few and relatively very large, rarely > 15, restricted to centre of disc; no central paxillar spinelets graduating to the spines:
    M–moderately large centrally but not more than ½ r, spaced and often extending on to the papular areas, graduating in size down to the central paxillar spinelets
    A–absent, only central paxillar spinelets on many disc and mid-radial arm plates, not > 1·5 mm long
4. Proximal abactinal plates:
    c–convex, parapaxilliform, butting loosely together, spinules clustered on the raised area, mean no. 10–12 or less
    f–flat or low convex, polygonal, butting more or less closely together, spinules covering most of the surface and more numerous, mean no. 15–20
5. Papular areas:
    PB–initiating from a single large median primary pore, becoming irregularly bilobed, sometimes indistinctly so
    PC–initiating from a single large median primary pore, becoming crescentic (horseshoe-shaped), V-shaped or bilobed with long lobes
    D–double, initiating from a pair of pores, one each side of the mid-line, forming two diffuse lobes, merging proximally only in large specimens, R > 70 mm
6. Largest marginal spines:
    a–Fourth superomarginal spine abruptly and conspicuously enlarged, fourth inferomarginal plate reduced and often lacking a spine
    e–Marginal spines fairly even in size or the fourth to seventh (according to size, only the fourth in smaller specimens) enlarged but graduated
7. Marginal spines, relative length:
    I–most inferomarginal spines longer than the corresponding superomarginal ones
    S–most superomarginal spines longer (at least on the proximal half of the arm)
8. Inferomarginal spinules at the upper end of the plate:
    g–graduated, several becoming more or less elongated, graduating to the accessory spine(s) or spinelets, profile rough
    u–fairly uniform, only some enlarged spinelets on the lower face of the plates, profile fairly smooth between the spines

9. Furrow margins of adambulacral plates:
  P–with acute angles prolonged into the furrow, <90°
  R–rounded or with angles obtuse or right-angled

10. Subambulacral spine number

11. Pedicellariae:
  A–actinal
  M–marginal
  D–dorsal

12. Maximum recorded R

As a result of these comparisons between the Atlantic species, two further supraspecific groups can be recognized within the genus *Cheiraster*.

Firstly, the essentially dual nature and different ontogeny of the papular areas in *Cheiraster mirabilis* and *C. blakei* compared with the other species of *Cheiraster,* in my opinion justifies at least a subgeneric distinction for these two species. The relatively small size of the papulae themselves, the marked size difference of some of the plates (including the primary ones) on the disc and arm bases and the development of spines several millimetres long on some of these plates provide supporting characters. At least two of the non-Atlantic species currently listed as *Luidiaster* can be placed in this subgenus, for which I propose the name *Christopheraster.* These are: *Pontaster oxyacanthus* Sladen, 1889, from Japan, which is very similar in abactinal armament to *C. blakei* and likewise has the small papular pores almost entirely offset from the midradii, and *Cheiraster horridus* Fisher, 1906, from the Hawaiian Islands, also with very small lateral papulae, a marked size difference of some of the abactinal plates and more or less enlarged spines on the larger plates (Fig. 2g & h). The holotype of *oxyacanthus* at R 73 mm has two large subambulacral spines on most plates, while that of *horridus* at R 35 mm has two subequal spines, so that the tendency to develop a second subambulacral spine, more or less accelerated in different species, may also be used to distinguish the subgenus.

Secondly, the unusual combination in *C. echinulatus* of rather low, polygonal, closely-fitting abactinal plates armed over most of their surface with relatively numerous short spinules, dorsally broad superomarginals, unlike *Cheiraster* (*Luidiaster*), usually slender marginal spines, unlike the conical ones of *Cheiraster* (*Cheiraster*), and multiple subambulacral spines in all but the smallest specimens (R <20 mm), also justifies a subgeneric distinction I believe. The name *Barbadosaster* (again reflecting the type locality of the type species) seems appropriate. In this case the subgenus appears to be monotypic. One non-Atlantic species of *Cheiraster—Pontaster teres* Sladen, 1889, from the Banda Sea, East Indies, superficially resembles *C.* (*Barbadosaster*) *echinulatus* in the slender marginal spines and multiple subambulacrals but differs markedly in the pore areas.

CHEIRASTER Studer

Archaster (pt.) Perrier, 1875 : 348 [1876 : 268] (*A. echinulatus*); 1884 : 256; Verrill, 1885*a* : 151.

Cheiraster Studer, 1883 : 129; 1884 : 49–50; Perrier, 1885 (pt.) : 70; 1894 : 275; Fisher, 1906 : 1040; Ludwig, 1910 : 440, 454–457; Fisher, 1911 : 120, 123; Verrill, 1915 : 123–124; Fisher, 1919 : 190–191; H. L. Clark, 1941 : 26; Downey, 1973 : 40–41; Jangoux, 1978 : 95, Walenkamp, 1979 : 23.

Luidiaster Studer, 1883 : 131 [nom. nud., no species named]; 1884 : 46–47; Ludwig, 1910 : 440–441, 451–454; Fisher, 1911 : 127; Verrill, 1915 : 149–150; Fisher, 1940 : 96; H. L. Clark, 1941 : 28. [Type species: *Luidiaster hirsutus* Studer, 1884.]

Pontaster (pt.) Sladen, 1885 : 610; 1889 : 23–27; Verrill, 1894 : 247; 1895 : 131.

Acantharchaster Verrill, 1894 : 268–269. [Type species: *Archaster dawsoni* Verrill, 1880.]

Pectinaster: Verrill, 1915 : 137–139; Downey, 1973 : 43; Walenkamp, 1979 : 26. [Non *Pectinaster* Perrier, 1885.]

TYPE SPECIES. *Cheiraster gazellae* Studer, 1883, by subsequent designation by Ludwig, 1910.

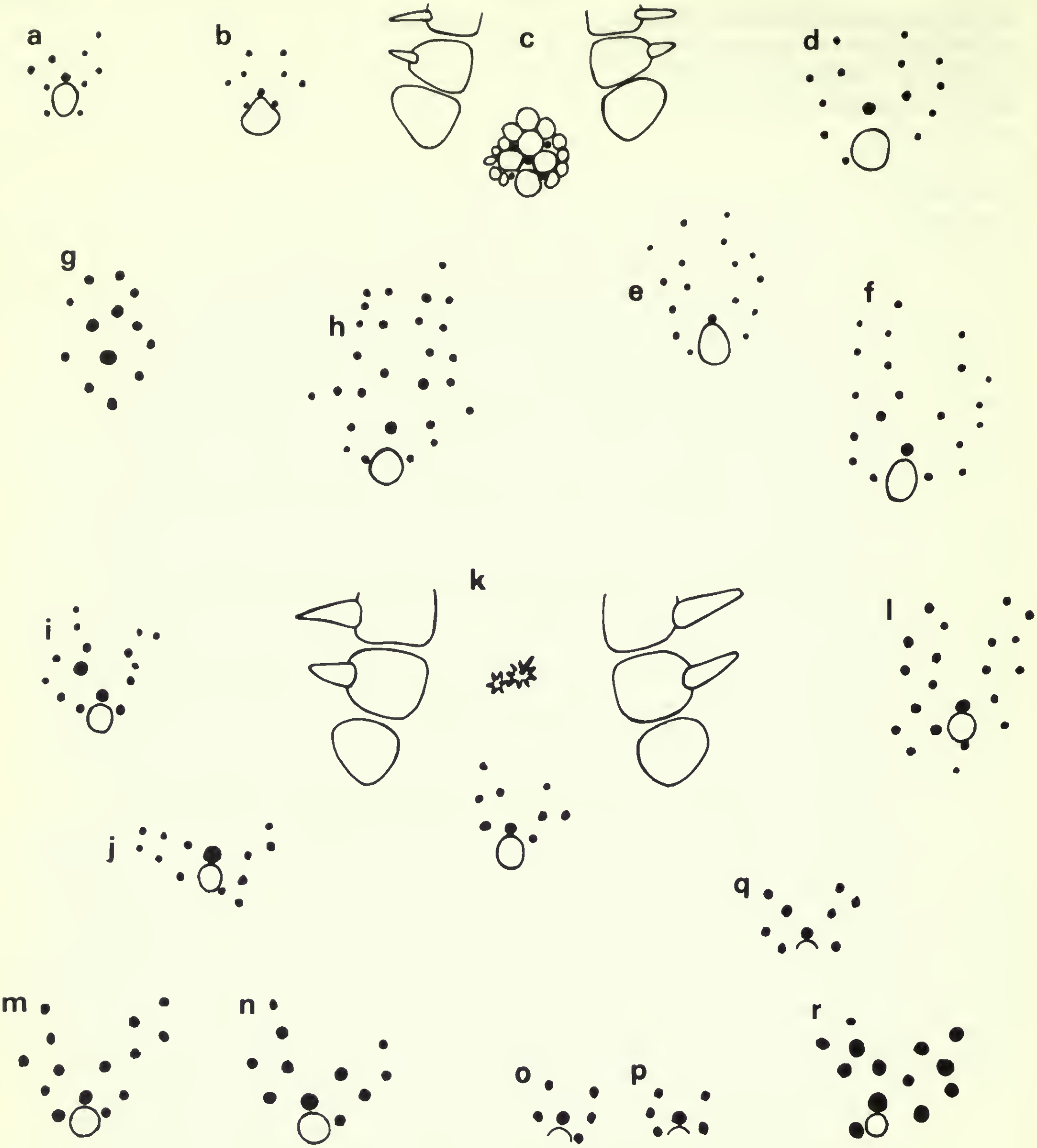

Fig. 4 Pore arrangements, showing presumed primary radial plates. (a–h) *Cheiraster (Barbadosaster) echinulatus* (Perrier). (a) *Blake* st. 45, MCZ 2181, R 27 mm; (b) *Albatross* st. 2322, USNM 10109, R *c.* 30 mm; (c) *Blake* st. 36, MCZ 24, R *c.* 20 mm (with proximal superomarginals); (d–f) *Atlantis* st. 2981C or 2982C, MCZ 3917, R 48, 47 and 51 mm; (g) holotype of *C. vincenti* Perrier, *Blake* st. 231, R *c.* 42 mm; (h) *Atlantis* st. 3480 or 3482, MCZ 3924, R *c.* 55 mm. (i–r) *Cheiraster (Cheiraster) sepitus* (Verrill), (i) 'topotype', *Albatross* st. 2075, USNM 24525, R *c.* 37 mm; (j) holotype of *Pectinaster dispar* Verrill, *Albatross* st. 2751, USNM 18468, R *c.* 50 mm; (k) *Albatross* st. 2531, USNM 12062, R 35–40 mm (with proximal superomarginals); (l) holotype of *Pontaster perplexus* Perrier, *Talisman* 1883, st. 96, PM 3378, R 52 mm; (m, n) holotype of *Luidiaster dubius* H. L. Clark, *Atlantis* st. 3326, MCZ 3815, R *c.* 60 mm; (o, p) *Princesse Alice* st. 743 (Azores), MCZ 2689, R 22 mm; (q) same sample (named *Pontaster venustus* by Koehler, 1909), R *c.* 33 mm; (r) *Talisman* 1883, st. 93, MCZ 30, R *c.* 45 mm (named *P. venustus* by Perrier, 1894).

(In fact, the spelling of the specific name in 1883 was *Gazella*, emended in 1884 to the genitive.)

A genus of Benthopectinidae without odd interradial marginal plates; abactinal plates usually parapaxilliform, more or less convex but flatter on the arms and sometimes all low, armed with several spinules, in most species many midradial and disc plates with a larger central spinelet, sometimes a spine >2 mm long; papular pores limited to a bilobed area at the base of each arm, or sometimes a pair of lateral areas loosely integrated at their proximal ends medially, rarely the two lobes not well defined or asymmetrical, undeveloped in younger animals, R <*c.* 30 mm, only the plates in the median proximal part of the area somewhat deepened; superomarginal plates aligned partially on the dorsal surface and forming a more or less broad frame to the paxillar area (except in *Cheiraster* (*Luidiaster*) where they are inconspicuous), armed usually with a single conical or spike-like spine on the dorso-lateral convexity; inferomarginal plates sometimes with more than one large spine or graduated spinelets below the main spine; adambulacral plates with the convex or angular furrow margins armed with a fan of slender furrow spines, the arc usually continuous with a few similar but smaller proximal and distal spines, partly surrounding one, two, or several, more or less enlarged subambulacral spines, similar in shape and size to the marginal spines; fasciculate pedicellariae usually present, at least on some actinal plates, often also abactinally and on the lower faces of the inferomarginals adjoining the adambulacrals, rare in a few species (e.g. *C. sepitus*), mostly bipectinate (i.e. arising from two adjacent plates) but the inferomarginal ones often lack an adambulacral component. Dorsal muscle bands of arms are attached proximally to one or two ambulacral plates, which may have modified ridges, the adjacent marginals and sometimes also to the dorsal body wall distal to the papular area.

Subgenus ***CHEIRASTER*** Studer, 1883

A subgenus with abactinal plates parapaxilliform convex and rounded, even those on the disc only abutting loosely together, most proximal and mid-radial ones armed with a central spinelet among the smaller spinules; papulae including a median proximal primary one, distinct from the rest (except in some larger specimens, R >50 mm) by its larger size and position, which is at first distal to the primary radial plate though may become dissociated from it as other plates develop, the later developed pores at first forming a median patch and then extending into a distal lobe on each side; superomarginal plates forming a more or less broad frame to the paxillar area in dorsal view; marginal spines conspicuous, conical or spike-like, some species with a second but smaller inferomarginal spine; adambulacral plates predominantly with single subambulacral spines, similar in shape to the marginal ones, though the first plate and some distal plates may develop a second large spine.

TYPE SPECIES. *Cheiraster gazellae* Studer, 1883. Philippines—NW Australia: 360–470 metres.

OTHER SPECIES INCLUDED. In chronological order:

Archaster sepitus Verrill, 1885	North and Central Atlantic	485–3700 metres
Pontaster pilosus Alcock, 1893	South of India	1080–1310 metres
C. inops Fisher, 1906	Hawaiian Is to Sri Lanka	430–1250 metres
C. snyderi Fisher, 1906	Hawaiian Is–Nicobar Is	420–1670 metres
C. niasicus Ludwig, 1910	Philippines–Celebes	485–930 metres
C. ludwigi Fisher, 1913	Indonesia	1270 metres
C. triplacanthus Fisher, 1913	Celebes & South-east Africa	1050–1280 metres
C. planus Verrill, 1915	Gulf of Mexico–French Guiana	550–715 metres
C. diomedeae Fisher, 1917	Philippines	770 metres
C. weberi Döderlein, 1921	Indonesia	470 metres
C. otagoensis McKnight, 1973	South New Zealand	1000–1280 metres

(A specimen from off Natal with R *c.* 40 mm referred to *C. triplacanthus* (A. M. Clark, 1977), has distinctly enlarged primary papular pores; Fisher (1919) noted only that the pore areas in the holotype (R 49 mm) are 'double and joined only at the adcentral end'.)

Subgenus *LUIDIASTER* Studer, 1884

A subgenus of *Cheiraster* with abactinal plates parapaxilliform, even those on the disc rounded and abutting loosely together or more or less spaced, most of the larger plates, even laterally on the arms, armed with a central spinelet among the smaller spinules; papulae including a median proximal primary one but this probably soon became indistinguishable as the number of pores increases and the areas spread, though are still bilobed; superomarginal plates aligned mainly laterally, inconspicuous dorsally; marginal spines conspicuous, conical or spike-like, usually at least two on most inferomarginal plates; adambulacral plates with two or more large subambulacral spines, the furrow angle variable.

TYPE SPECIES. *Luidiaster hirsutus* Studer, 1884. Kerguelen, South Africa & Bouvet I.; 240–550 metres.

OTHER SPECIES INCLUDED. In chronological order:

Archaster dawsoni Verrill, 1880	Bering Sea–British Columbia	100–290 metres
Pontaster planeta Sladen, 1889	S. Chile, Argentina–Falklands	350–450 metres
Cheiraster gerlachei Ludwig, 1903	Antarctic	160–810 metres
Pectinaster robustus A. H. Clark, 1917†	Chile	2410 metres
Luidiaster tuberculatus Djakonov, 1929	Japan Sea	140–850 metres

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† See p. 121.

Subgenus *BARBADOSASTER* nov.*

A subgenus of *Cheiraster* with most proximal abactinal plates polygonal in outline, fitting closely together and not markedly convex, sometimes almost flat, armed with relatively numerous short spinules, on the larger plates often forming two rings around a central spinelet; papulae including a median proximal primary one, usually distinct from the rest by its size and position, the later developed pores forming at first a median patch, then extending distally into a lobe on each side, though the two lobes may be unequal or ill-defined, hardly separated medially; superomarginal plates forming a broad frame to the paxillar area in dorsal view; marginal spines slender, not very stout basally, single, though some enlarged spinelets develop below the inferomarginal spine; most adambulacral plates with more than one subambulacral spine, except in very small specimens, R <20 mm, the furrow angle of the proximal plates markedly acute.

TYPE SPECIES. *Archaster echinulatus* Perrier, 1875. South Florida—Caribbean; 150–570 metres. Monotypic.

Subgenus *CHRISTOPHERASTER* nov.*

A subgenus of *Cheiraster* with the abactinal plates parapaxilliform (but in *C. mirabilis* only slightly convex), distal plates more or less spaced, the proximal plates mostly fitting fairly closely, very variable in size, the primary central, radial and interradial plates particularly enlarged, some or most of the larger plates armed with a central spine >2 mm long, often conspicuous, surrounded by small spinules, some other plates may have a central spinelet

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*Named after the type localities of the relevant type species: Barbados for *C. (B.) echinulatus* and St. Christopher's (Kitts) for *C. (C.) mirabilis*.

but not in *C. mirabilis*; no primary midradial papular pore, the first-formed papulae a pair, each latero-distal to the primary radial plate, later pores developing laterally and distally, the two pore areas on each ray only loosely meeting proximally in larger specimens to form a single diffuse bilobed area with few, if any, midradial pores, the pores themselves relatively small and hardly visible with the naked eye, relatively numerous (*c.* 100 at R 100 mm on each ray); superomarginal plates partly aligned dorsally, forming a narrow frame to the abactinal area but becoming inconspicuous in the largest specimens (R > 120 mm); marginal spines large and spike-like; adambulacral plates with one or two large subambulacral spines, sometimes two only in the largest specimens, furrow angles variable in prominence.

TYPE SPECIES. *Archaster mirabilis* Perrier, 1881. Florida—Windward Is; 380–730 metres.

OTHER SPECIES INCLUDED. In chronological order:

Cheiraster blakei sp. nov.	Florida–Northern Brazil	250–1030 metres
Pontaster oxyacanthus Sladen, 1889	Southern Japan	630 metres
C. horridus Fisher, 1906	Hawaiian Is	260–330 metres

This leaves a residue of the following species of uncertain affinities which have been referred to *Cheiraster* or *Luidiaster*:

Cheiraster pedicellaris Studer, 1883. NE of Australia; 1000 metres. The holotype has R *c.* 30 mm and is probably a young specimen of *C. gazellae* according to Ludwig (1910).

Pontaster subtuberculatus Sladen, 1889. SE of Australia; 1740 metres. The holotype has R only *c.* 24 mm. Like *Christopheraster* it has no mid-radial papulae, the 17–21 pores forming two irregular longitudinal rows on each side, but the pores are relatively large and there is no sign of any enlarged spinelet or spine on any abactinal plates. The arms are unusually short for a *Cheiraster* and the single marginal spines are remarkably short and blunt.

Pontaster teres Sladen, 1889. Indonesia; 260 metres. The holotype has R 42 mm and superficially resembles *C. (Barbadosaster) echinulatus,* the superomarginals being relatively broad and the marginal spines unusually slender. However, denuding part of the paxillar area shows an unusual combination of larger convex plates with flattened interstitial ones between, fitting closely together except where the relatively large papular pores are developed, at the *sides* of the arm bases. The subambulacral spines are multiple.

Pontaster trullipes Sladen, 1889. Philippines; 1920 metres. The holotype has R only 27 mm. The primary radial and interradial plates are enlarged, as in *Christopheraster,* but no large spines occur and the papulae form a median group, in which no primary one is distinct.

Pontaster cribellum Alcock, 1893. Laccadive Sea; 2200 metres. The holotype has R 45 mm. It is said to resemble *P. subtuberculatus* in lacking spinopaxillae and having relatively broad superomarginals but the papularia are small and compact, with only 5 or 6 papulae in each and the marginal spines are sharp.

Marcelaster antarcticus Koehler, 1907 (referred to *Luidiaster* by Fisher, 1940). South Orkney Is.; 3250 metres. R in the type series is up to only 33 mm. The proximal plates appear rather variable in size in the poor drawing and there are some relatively large disc spines but the papulae were not described at all so the position must remain uncertain.

Cheiraster granulatus Ludwig, 1910. 'Indian Ocean'; depth not given. Ludwig's *Valdivia* report was never completed and the only information on this barely established species is in the key distinguishing it from *C. subtuberculatus* by the numbers of inferomarginal and furrow spines and the occurrence of actinal pedicellariae, which could all be correlated with a size difference, if it was appreciably larger than the small type of *C. subtuberculatus.*

Cheiraster yodomiensis Goto, 1914 (referred to *Luidiaster* by Hayashi, 1973). Japan; 160 metres. The holotype has R 170 mm and closely resembles a *Nearchaster* in the many disc spines, laterally aligned superomarginals and great extent of the papular pores along the sides of the paxillar areas. Also the interradial superomarginal spines are relatively large and possibly asymmetrical in some interradii, judging from the photograph.

Cheiraster richardsoni Fell, 1958. Cook Strait, New Zealand; 730 metres. The holotype has R 31 mm. The superomarginals are broad dorsally and the subambulacral spines single. The papulae were undescribed.

Cheiraster monopedicellaris McKnight, 1973. Northern New Zealand; 720–770 metres. The holotype has R 39 mm. The superomarginal plates are very broad but some abactinal plates have enlarged spinelets, unlike *C. subtuberculatus*. The 3–5 papulae are said to be in a more or less V-shaped arrangement.

The complex synonymies of the North and Tropical Atlantic species are as follows:

Cheiraster (Barbadosaster) echinulatus (Perrier)

Figs 3a–f, 4a–h

Archaster echinulatus Perrier, 1875 : 348 [1876 : 269]; 1884 : 263–264, pl. 10, fig. 4.
Archaster mirabilis (pt) Perrier, 1884 : 258–259 (sts 143 & 231).
?*Cheiraster mirabilis:* Perrier, 1894 : 276–278, pl. 20, fig. 4.
Cheiraster vincenti Perrier,.1894 : 275–276.
Cheiraster echinulatus: Perrier, 1894 : 278; Verrill, 1915 : 129–130 (non pp. 131–133, pl. 14, fig. 3, pl. 19, fig. 2, pl. 25, fig. 1 ? = *C. blakei*); Downey, 1973 : 42, pl. 13, figs C, D.
Pontaster oligoporus Perrier, 1894 : 293.
Luidiaster vincenti: Ludwig, 1910 : 452, 453.
Pectinaster echinulatus: Ludwig, 1910 : 449.
Pectinaster mixtus Verrill, 1915 : 140–145, pl. 6, fig. 2, pl. 15, fig. 2, pl. 17, fig. 1; Macan, 1938 : 349 (listed); Downey, 1973 : 43–44, pl. 14, figs C, D.
Pectinaster vincenti: Verrill, 1915 : 139–140; Macan, 1938 : 349 (listed).
Pectinaster oligoporus: Verrill, 1915 : 147–148; Macan, 1938 : 349 (listed).
Luidiaster mixtus: H. L. Clark, 1941 : 29–30; A. H. Clark, 1954 : 375 (listed).

TYPE LOCALITY. Barbados, 183 metres.

RANGE. Gulf of Mexico, Florida Strait, south to Nicaragua and Venezuela, east to the Leeward Islands; 150–570 (?586) metres. (The *Atlantis* specimen from 1000 fathoms E of Cuba said by H. L. Clark (1941) to show some anomalous features, is referable to *C. sepitus*, having convex spaced abactinal plates with relatively few spinules, stout conical marginal spines, single conical subambulacral spines and relatively few, *c.* 6, furrow spines in obtusely angled series.)

Cheiraster (Christopheraster) mirabilis (Perrier)

Fig. 2a, b

Archaster mirabilis Perrier, 1881 : 27 (paragraphs 1–4 only); 1884 : 256–258, pl. 9, fig. 4 (non pp. 258–259, sts 231 & 143, pl. 10, fig. 3 = *C. echinulatus*) ?pl. 10, fig. 2 (or = *C. blakei*).
Archaster coronatus Perrier, 1884 : 262–263 (non st. 19 = *C. blakei*).
Cheiraster coronatus: Perrier, 1894 : 271–275; Ludwig, 1910 : 455, 456.
Cheiraster mirabilis (pt) Verrill, 1915 : 124–127 (non pl. 14, fig. 5 = *C. blakei*; non *C. mirabilis*: Downey, 1973, Walenkamp, 1979 = *C. planus*).
Cheiraster enoplus Verrill, 1915 : 135–137, pl. 18, fig. 1 (non *C. enoplus*: Downey, 1973 nec *Luidiaster enoplus*: H. L. Clark, 1941 = *C. blakei*)

TYPE LOCALITY. St. Kitts, Leeward Islands, 380 metres.

RANGE. SE Florida to the Windward Islands (records from the Gulf of Mexico probably mistakes for other species); 380 (?265)—1470 (usually 400–700) metres; deeper records, e.g.

Blake st. 196, 1030 *fathoms*, may be for *C. sepitus*. Uncertain identity precludes inclusion of lesser *Blake* station depths.

Cheiraster (Christopheraster) blakei sp. nov.

Figs 1b, 2c–f

Archaster coronatus (pt) Perrier, 1884 : 262 [st. 19 only].
?*Archaster mirabilis* (pt) Perrier, 1884, pl. 10, fig. 2 (non *A. mirabilis* Perrier, 1881).
Cheiraster mirabilis (pt) Verrill, 1915, pl. 14, figs 5, 5a.
Cheiraster echinulatus (pt) Verrill, 1915 : 131–133, pl. 14, fig. 3, pl. 19, fig. 2 [?pl. 25, fig. 1].
Cheiraster coronatus: H. L. Clark, 1941 : 26–27; A. H. Clark, 1954 : 375 (listed) (non *C. coronatus*: Perrier, 1894, Ludwig, 1910 = *C. mirabilis*).
Luidiaster enoplus: H. L. Clark, 1941 : 28–29 (non *C. enoplus* Verrill, 1915 = *C. mirabilis*).
Cheiraster enoplus: Downey, 1973 : 42–43, pl. 14, figs A, B.

DESCRIPTION OF HOLOTYPE. R of the only entire original arm is 118 mm (two arms with regenerating tips are 95 mm or less); r is 12 mm; R/r = 9·8/1. Arm breadth at the fifth superomarginals is 9·2 mm and the paxillar breadth here 6·0 mm, or 65%. The arms taper hardly at all for the first third of their length.

There are about 35 spines more than 2 mm long on the disc based on enlarged abactinal plates including the primary radial and interradial plates and others. An additional 10–12 smaller spines/spinelets arise in the papular area on the base of each ray, mostly on the row of plates between the two main irregular lines of pores each side of the midradial line. The longest central spines are 3·6 mm long. Only a few other abactinal plates have an enlarged central spinelet among the small slender tapering spinules, length : basal breadth *c.* 2·5 : 1. These number usually 6–14, according to the plate size, mean *c.* 10, but the enlarged disc plates have up to 20 spinules around the central spine. All the abactinal plates are markedly convex and may be called parapaxilliform; they are rounded or slightly polygonal and only butt loosely together over most of the disc, while those on the arms are spaced from each other. The papulae number *c.* 75 on each ray; only one or two proximal ones (if any) are midradial, the rest being arranged in two distally diverging bands extending from alongside the primary radial plate to level with the distal ends of the third superomarginal plates.

There are 55 superomarginals on the intact original arm, framing the paxillar area narrowly, each armed with a single spine of moderate size, the longest on the fifth and sixth plates up to 4·0 mm long, basal breadth *c.* 0·7 mm. The corresponding inferomarginal spines are similar or slightly longer, with an accessory spine about two-thirds as long below it, often also a third still smaller spine on the proximal plates besides several slender spinelets on the ventral face of the plate among the fine spinules which are of various sizes; the whole armament gives a hirsute or shaggy appearance to the plate as viewed from below.

The actinal areas are small and triangular with four or five plates along the midinterradial line on each side of which the irregular adradial series numbers only about seven plates, those bearing the pedicellariae enlarged. The actinal armament is very sparse and mixed in size with only about two spinelets/spinules on most plates.

Only 13½–15 adambulacral plates correspond to the first 10 inferomarginals. On each adambulacral no more than eight spines project over the furrow, their bases usually forming an angle of *c.* 90° but this may be blunted. The subambulacral spines are single, much larger and accompanied by only a few small spinules on the ventral face of the plate. The oral plates have 10 or 11 furrow spines, the apical one much enlarged and the second one intermediate. Probably only one suboral spine is enlarged but the plates are badly rubbed and most spines lost.

Pectinate pedicellariae are developed on the adradial actinal plates (usually four in each interradius), on the ventral sides of the inferomarginals adjacent to the adambulacrals (for about three-quarters of the arm length) and abactinally (but only two are present near the centre of the disc).

VARIATIONS. Some indications of variations and growth changes can be derived from Table

Table 4 *Cheiraster (Christopheraster) mirabilis* (Perrier). Measurements (in mm) and counts from various specimens including the holotypes of *C. enoplus* Verrill (the first specimen) and *mirabilis*, data from Verrill and Perrier respectively.

Station	R	r	R/r	No. of pores/ray	No. of disc spines	No. of s.m. plates	Length of 4th s.m. spine	No. of furrow spines	No. of subamb. spines
Alb. st. 2128 (Verrill)	185	21	8·8	400+ [?]	*c.* 15	*c.* 60	15	10–12	1 to 2
Gerda st. 917	110	13	8·5	88	9	49	–	10,11	1
Gerda st. 694	105	12·5	8·4	*c.* 80	10	58	13	12	1
Gerda st. 1012	*c.* 95	12	*c.* 8	98	6	40+	–	9	1
Blake Holotype (Perrier)	87	12	7·25	*c.* 73	6–10	40+	–	10	1
Pillsbury st. 944	85	10	8·5	*c.* 95	7	47	–	10	1
Pillsbury st. 918	82	10·5	7·8	58	4	46	–	9	1–1 (2)
Atlantis st. 3444	72	–	–	39	5	–	12	–	–
Pillsbury st. 889	70	8·5	8·2	*c.* 48	12	39	–	9	1 (2)
USNM no. 3741, Puerto Rico	*c.* 68	9	*c.* 7·5	50–60	7	–	–	–	1
Gerda st. 235	68	9	7·5	39,41	18	38	9·7	9,10	1 (2)
Pillsbury st. 891	50	·7	7·1	31	7	36	–	9	1 (2)
Gerda st 694	*c.* 45	6	*c.* 7·5	27,28	2	–	6·3	8–10	1
Gerda st. 694	39	5	7·8	17	5	30	2·8	7,8	1
Gerda st. 1008	31	5	6·2	18	6	26	*c.* 3·5	7,8	1

Table 5 *Cheiraster (Christopheraster) blakei* sp. nov. Measurements (in mm) and counts from various specimens.

Station	R	r	R/r	No. of pores/ray	No. of disc spines	No. of s.m. plates	Length of longest s.m. spine	No. of furrow spines	No. of subamb. spines
Pillsbury st. 607	*c.* 130	15	*c.* 6·7	*c.* 160	few	–	*c.* 6	–	1
Gerda st. 918 Holotype	118	12	9·8	*c.* 75	35+	55	4·0	7,8	1
Atlantis st. 2963F	112	13	8·6	*c.* 80	*c.* 75	–	5·5	8,9	(1) to 2
Pillsbury st. 607	*c.* 110	13	8·5	*c.* 80	*c.* 16	–	*c.* 5	*c.* 9	1
Gerda st. 403	77	11	7·0	*c.* 66	*c.* 16	39	3·8	*c.* 9	1
Oregon st. 4226	*c.* 70	12	*c.* 5·8	56	–	–	*c.* 4	*c.* 10	2 (1)
Gerda st. 403	65	10	6·5	73	17	38	3·3	7	1
Gerda st. 403	63	9	7·0	29	*c.* 14	36	2·6	9	1
Oregon st. 4226	45	8	5·6	–	*c.* 7	–	–	*c.* 9	1 (2)
Gerda st. 403	45	8	5·6	*c.* 27	*c.* 14	30	–	7 (8)	1
Gerda st. 403	44	7·5	5·9	34	17	28	3·4	8	1
Silver Bay st. 1184	38	8·5	4·5	33	22	27	3·2	9	1
Pillsbury st. 587	33	7·0	4·7	14	*c.* 18	26	–	8	1

5. The disc is usually relatively larger than in the holotype and the arms more often taper evenly from the base, with the superomarginals forming a somewhat wider frame to the paxillar area, though never making up as much as 50% of the arm breadth. Often many abactinal paxillae have an enlarged central spinelet, graduating in size to the small spines on the papular areas. The relative number of papulae also varies; one specimen has well over 100/ray even though R does not exceed 100 mm. In small specimens, the first one or two pores appear at R *c.* 16 mm (at the same time as the genital pores which are adjacent to the first superomarginal plates). 20 specimens with R 14–19 mm show a range in pore/ray number of 0–11 but with a mean of only 3. The marginal spines may be relatively larger than in the holotype, up to *c.* 6 mm long at R >100 mm. In small specimens the fourth superomarginal spine is the largest but the fifth and sixth ones grow allometrically to equal and then exceed it. The number of adambulacral plates corresponding to the first ten inferomarginals is usually more than in the holotype, often 16 or up to 18 being noted. The bases of the furrow spines usually form a more pronounced angle projecting over the furrow. Finally, the occurrence of pedicellariae varies; some specimens may have more numerous abactinal ones; also at least one was observed with inter-superomarginal pedicellariae interradially.

AFFINITIES. *Cheiraster (Christopheraster) blakei* is closely related to *C. (C.) mirabilis.* Most of the differences are expressed in the tabular key (Table 3), the numerical tables here (Tables 4 and 5) and the comparison on pp. 104–5. These can be summed up as differences in armament, *C. mirabilis* having the enlarged abactinal and marginal spines relatively larger but fewer than *C. blakei* and the abactinal and inferomarginal spinules short and more nearly uniform. Additionally, the furrow spines tend to be more numerous in *C. mirabilis,* their arrangement on the furrow margin less angular and the contours of the abactinal plates lower.

TYPE LOCALITY. *Gerda* st. 918, 26° 03′ N, 78° 05′ W, between Florida and the Bahamas, 804–822 metres. To be deposited in the U.S. National Museum.

RANGE. Recorded from SE of Florida and the coasts of Cuba east and south to the Lesser Antilles and northern Brazil at least as far east as 44° W; 250 (?225)–1033 (but mostly 500–800) metres.

Cheiraster (Cheiraster) planus Verrill

Fig. 5a, b

Cheiraster planus Verrill, 1915 : 133–135, pl. 18, fig. 2.
Pectinaster gracilis Verrill, 1915 : 145–147, pl. 6, fig. 1, pl. 14, fig. 4, pl. 15, fig. 1; Macan, 1938 : 349 (listed); Jangoux, 1978 : 95–96, fig. 2A, B. (?*P. gracilis*: Walenkamp, 1979 : 26–30, figs 9, 10, pl. 5, figs 1–4, pl. 6, figs 1–4).
Cheiraster mirabilis: Downey, 1973 : 41–42, pl. 13, figs A, B; Walenkamp, 1979 : 23–26, figs 8, 10, pl. 4, figs 2–4 (non *C. mirabilis* (Perrier, 1881)).

TYPE LOCALITY. Unknown to Verrill but the holotype (USNM 18469) may have been from *Albatross* st. 2396 (Gulf of Mexico between the Mississippi delta and Cedar Keys) from which there is a sample (USNM 10564) including another specimen of *C. planus* (named *mirabilis* by Verrill but probably at an earlier date) and a note saying ‘17 specimens lent to A. E. Verrill’.

RANGE. Western Gulf of Mexico and SW Caribbean, eastwards south of Jamaica to the Lesser Antilles and along the north coast of South America to French Guyana; 550 (?408)–715 (?824) metres. A record from SW of Florida, *Gerda* st. 439, *c.* 24° N, 82½° W, needs confirmation since even the larger of the two specimens has R only 16 mm; the superomarginal spines appear to be larger than the inferomarginal ones, the abactinal plates are convex, the inferomarginals have fairly uniform spinules and the furrow angles of the adambulacrals are relatively shallow, as in *C. planus* as opposed to *C. echinulatus.* However, most of the distinctive subambulacral spines are lost.

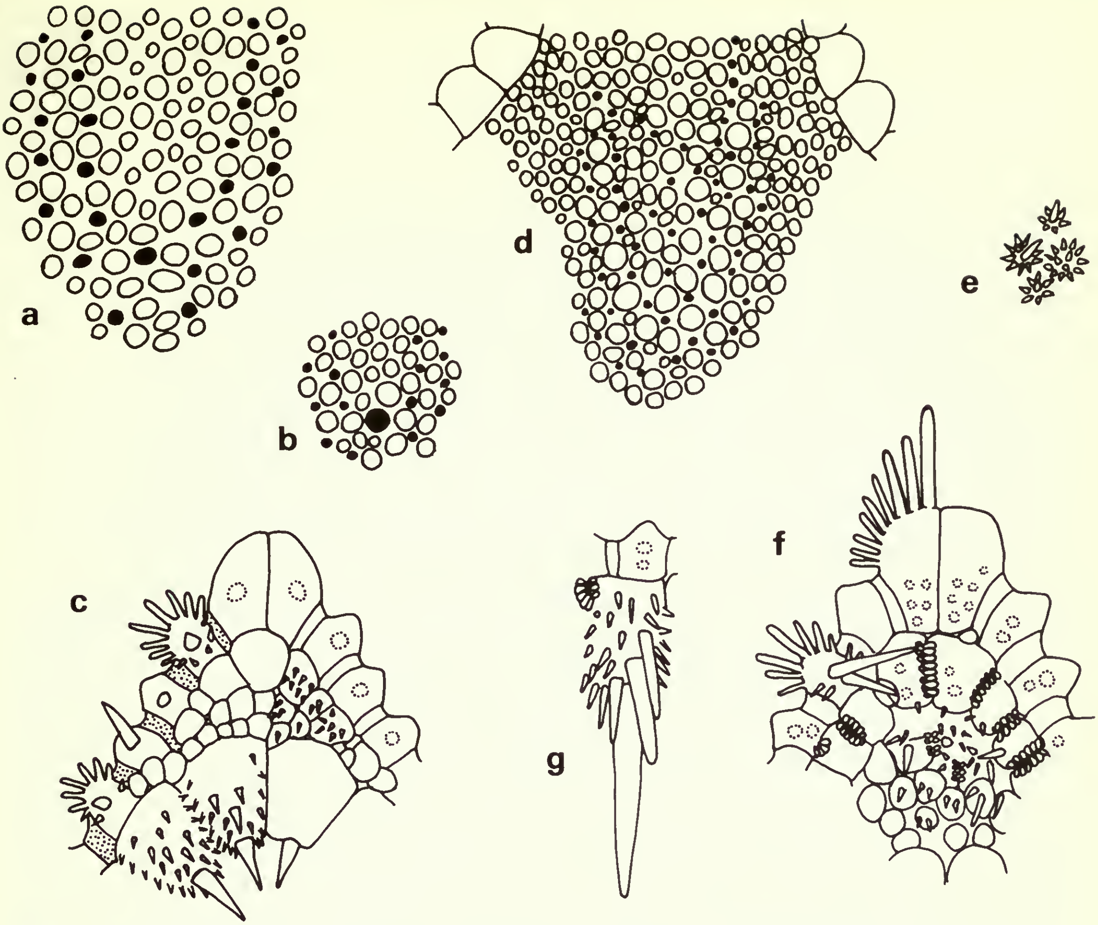

Fig. 5 (a, b) Pore areas of *Cheiraster (Cheiraster) planus* Verrill; (a) holotype, *Albatross* (st. ?), USNM 18469, R 92 mm; (b) *Albatross* st. 2396, USNM 10564, R *c.* 60 mm (same sample as holotype of *Pectinaster gracilis* Verrill); (c) *Cheiraster (Cheiraster) sepitus* (Verrill), ventral interradius partly denuded, same specimen as in fig. 4(k), the sockets of the missing subambulacral and suboral spines dotted; (d–g) *Cheiraster (Luidiaster) robustus* (A. H. Clark), holotype, *Albatross* st. 2789 (Chile), USNM 36945; (d) papular area and adjacent second and third superomarginals; (e) armament of four proximal abactinal plates; (f) ventral interradius, armament partly reconstructed, mostly lost; (g) fourth inferomarginal and adjacent adambulacral plates.

Cheiraster (Cheiraster) sepitus (Verrill)

Figs 4i–r, 5C

Archaster sepitus Verrill, 1885*a* : 151.

Pontaster venustus Sladen, 1889 : 52–55, pl. 8, figs 5, 6, pl. 12, figs 5, 6; Perrier, 1894 : 287–288; 1896 : 47; Koehler, 1909 : 14–15, pl. 1, fig. 13; Mortensen, 1927 : 71.

Pontaster venustus var. *robusta* Sladen, 1889 : 55.

Pontaster sepitus: Verrill, 1894 : 247; 1895 : 137; 1915 : 130 (footnote).

Pontaster perplexus Perrier, 1894 : 288–290, pl. 21, fig. 1, pl. 22, fig. 1; Mortensen, 1927 : 72.

Pectinaster echinulatus (pt) Ludwig, 1910 : 449 (*sepitus* a synonym).

Pectinaster dispar Verrill, 1915 : 148, pl. 14, fig. 1; Macan, 1938 : 349 (listed).

Pectinaster venustus: Koehler, 1924 : 186.

Luidiaster dubius H. L. Clark, 1941 : 30, pl. 2, fig. 2.

Luidiaster mixtus (pt) H. L. Clark, 1941 : 29–30 (specimen from 1000 fathoms).

TYPE LOCALITY. S of Cape Sable, Nova Scotia; 1570 metres.

RANGE. South of Nova Scotia south to Cuba and the Lesser Antilles, east to the Azores, Bay of Biscay [? no details, Koehler, 1924], Portugal and south to the Cape Verde area; 485–3703 metres (mostly 1000–2000 metres).

PECTINASTER Perrier

Pectinaster Perrier, 1885 : 70; 1894 : 278–279; Ludwig, 1910 : 448–451 (pt); Fisher, 1911 : 122–123; 1919 : 182; Macan, 1938 : 348–349 (pt). (non *Pectinaster*: Verrill, 1915, Downey, 1973).
Pontaster (pt) Sladen, 1889 : 43–52.

TYPE SPECIES. *Pectinaster filholi* Perrier, 1885, by subsequent designation by Ludwig, 1910. No type species was designated by Perrier in 1885 when he included two species, *Archaster insignis* Perrier, 1884 and *P. filholi* which was evidently new (though not so stated), the genus being diagnosed only by the presence of fasciculate pedicellariae (though these are relatively simple in *insignis* having up to only four spinose 'valves'). In 1894 Perrier referred *P. insignis* to *Dytaster* Sladen, 1885, leaving *P. filholi* by elimination as the only eligible type species for *Pectinaster,* the formal designation awaiting Ludwig (1910 : 449).

DIAGNOSIS. A genus of Benthopectinidae with no odd interradial marginal plates (though the paired first marginals may be a little asymmetric in some interradii of some individuals), the interradial marginal spines relatively small; abactinal plates small paxilliform, at least the proximal ones elevated medially into a more or less well defined column bearing several spinules, on most plates of the disc and midradially on the arms surrounding a larger central spinelet, the spinules tending to form a continuous surface proximally in well-preserved (and probably in live) specimens; papulae restricted to an elongate oval papularium on to each arm base, formed of specialized markedly deepened abactinal plates, convex at the upper end and abutting together laterally with flanges to accommodate the papulae (see Fig. 1a), the surface of the papularium tending to bulge upwards (at least in preserved specimens when the dorsal body wall is contracted on to the ambulacra), the first-formed pores often forming transversely-aligned pairs, three or more pores developed by a size of R 20 mm; superomarginal plates mainly aligned laterally, only forming an inconspicuous rim to the paxillar area in dorsal view, each armed with an acute conical spine at the upper end; adambulacral plates with a single large conical subambulacral spine, only the first plate sometimes with a second spine; fasciculate pedicellariae usually present, often numerous, occurring on some abactinal, marginal, actinal and even a few adambulacral plates, usually oval in outline and formed of three or more modified spinelets based on either one or (pectinate pedicellariae) on two, rarely three, plates, the valves surrounding a deep hollow or bevelled notch in the plate or plates. Dorsal muscle bands of arms attached proximally to the wings of one or two ambulacral plates laterally and the adjacent marginal plates.

REMARKS. This diagnosis emphasizing the highly modified compact oval papularia, paxilliform abactinal plates and laterally-aligned superomarginal plates not forming a wide border to the paxillar area in dorsal view, restores *Pectinaster* to the restricted concept of Perrier in 1894. As discussed under *Cheiraster*, the inclusion in *Pectinaster* of *Archaster echinulatus* Perrier, 1875, *Pontaster cribellum* Alcock, 1893, *A. sepitus* Verrill, 1885 and *Pontaster venustus* Sladen, 1889 (the last two as synonyms) by Ludwig (1910), followed by Verrill's addition in 1915 of *Pectinaster gracilis, dispar* and *mixtus* (all new nominal species) and *Pontaster oligoporus* and *Cheiraster vincenti*, both of Perrier, 1894, broadened the genus to include species with less specialized papular areas and dorsally broad superomarginal plates. All these I consider have closer affinity with the type species of *Cheiraster, C. gazellae* Studer, 1883. The type material of most of them is relatively small so that the papulae have not yet formed bilobed areas, though the enlarged median proximal pore indicates that they are potentially bilobed.

The elimination of these leaves *Pectinaster* in the Atlantic represented only by *P. filholi* and *P. pristinus* (Sladen), though the status of *P. forcipatus* (Sladen) as distinct from *P. filholi* has been debated.

In 1910, Ludwig referred *Pontaster forcipatus* Sladen, 1889, from off the eastern U.S.A., to the synonymy of *Pectinaster filholi*, type locality off Cap Blanc (with a paratype from the Azores area). He was followed in this by H. L. Clark (1923) but in 1962 I challenged this synonymy on the grounds of apparent differences in the numbers of actinal plates and their armament in the type series of *P. forcipatus* and *P. forcipatus* var. *echinata* (the latter from the Crozet Is area of the Southern Ocean), compared with Perrier's description and figures of *P. filholi* supported by a specimen (R only 33 mm) in the British Museum collections from SW of Ireland. However, after seeing further NE Atlantic specimens collected by the *Discovery*, in 1976 (Clark & Courtman-Stock) I came to agree with Ludwig and synonymize both *forcipatus* and *echinatus* with *P. filholi*, which name I used for specimens from South Africa, following H. L. Clark. Not only is there considerable variation in the numbers and shapes of the actinal plates in specimens from various parts of the Atlantic but also the records of Sibuet (1975) from the Gulf of Guinea and off Angola provide a zoogeographical link between *filholi* from NW Africa and *echinatus* from the Cape and Southern Ocean. Perrier's illustration of *P. filholi* (1894, pl. 20, fig. 3b) shows oral plates of exaggerated size at the expense of the actinal area, which appears exceptionally small, only *c.* 35% of the oral plate length, measured interradially. In four *Discovery* specimens from the Cap Blanc area (st. 9133/5) an actinal area of each measures 61, 68, 74 and 95% of the oral plate length. This compares with three specimens from W of Ireland with values of 48–92% (the minimum predictably in the smallest specimen with R only 40 mm), ten from the Gulf of Guinea off Ghana with 60–90%, six from off the U.S.A. with 65–109% and six from off South Africa and the Crozet Is area with 76–115%. The specimens with the relatively largest actinal areas, interradially longer than the oral plates, are mostly large, R > 70 mm (see Table 6).

Sladen distinguished the variety *echinata* from the type material of *P. forcipatus* by the stouter marginal spines and larger central paxillar spinelets, the occurrence of which he thought was more widespread on the lateral paxillae. In the two largest syntypes of *echinata* (R *c.* 80 mm) the fourth superomarginal spine is 1·25 and 1·15 mm in basal breadth, the latter measurement being equalled in a South African specimen with R 72 mm. In North Atlantic specimens these spines are up to 0·9–1·0 mm—a small difference but just appreciable with the naked eye. Similarly, the longest central paxillar spinelets on the disc measure 1·0 mm or more in the southern specimens as opposed to usually 0·8–0·9 mm in the northern ones, though one syntype of *P. forcipatus* has spinelets up to 1·1 mm. The extent of the central spinelets on the lateral paxillae varies also in *P. mimicus* from the Indo-West Pacific and *P. agassizi* from the East Pacific and I do not think it is a character of specific weight. Nevertheless there may be sufficient justification in the relative spinelet size for treating the southern specimens as subspecifically distinct from *P. filholi* but this should await comparison with material from the southern part of West Africa.

One regional variation which may be significant is the relative number of pores in the papularia. In the available material this reaches a maximum of 20 in the american specimens and 21 in the NE Atlantic ones. The figured syntype(s) of *P. filholi* (Perrier, 1894, pl. 20, figs 3a, 3d) shows 7 pores (only 6 in the description). A syntype in the MCZ, Harvard, with R only *c.* 45 mm, also from the Cap Blanc area, has 10 pores in one area examined. However, a *Discovery* specimen from this vicinity has as many as 21 pores in one area and 18 in another at R 65–70 mm. An even higher number is shown by some specimens of a large sample taken off Ghana by the *Pillsbury* (*c.* 4° N, 2½° W), of which 22 specimens with r > 8 mm (R probably 40+ mm) have 11–27 pores, mean 19. This compares with 6–20 pores and a mean of only 10 in 16 american specimens. Unfortunately the *Pillsbury* material is dried and in poor condition so other characters such as spinelet length cannot be ascertained in many specimens. Even in spirit-preserved specimens of *Pectinaster*, owing to frequent breakage of the arm tips, few accurate estimates of R/r or counts of marginals can be made. The mean R/r value for 16 of the type series of *P. forcipatus* is 5·9/1, compared with 5·5/1 in six

Table 6 *Pectinaster filholi* Perrier. Measurements and counts from specimens from various parts of the range. The furrow spine number and length of the central paxillar spinelets are both maxima; the actinal plate number is along the interradius. The number of adambulacral plates corresponding to the first ten inferomarginals ranges from 15–19, usually 16–18, in all the areas.

Specimen	R	r	R/r	No. of pores	4th s.m. spine br.	Act. l./ oral l.%	Furrow spines	Act. pls /IR no.	L. pax. spinelets
Cap Blanc area:									
Holotype (Perrier)	64	10	6·4	5,6 (7)	–	–	7	2	–
Discovery 9133/5	40 + (?*c.* 70)	13	–	*c.* 12	0·92	74	8	4	0·75
Discovery 9133/5	62 + (*c.* 65)	12	*c.* 5·4	18,21	0·85	95	7	5	0·85
Discovery 9133/5	28 + (?*c.* 50)	9	–	8	–	61	7	–	–
Talisman st. 96	*c.* 45	9·5	*c.* 4·7	10	–	–	–	–	–
W & NW of Ireland:									
Discovery 7711/85	80	14	5·7	*c.* 9	1·00	92	7	3	0·83
Discovery 7711/85	62	11	5·6	11,14	–	–	–	–	–
Discovery 7709/73	41	8	5·1	*c.* 6	–	48	5 (6)	–	–
Discovery 7709/52	40	8	5·0	6,7	–	77	6	–	–
NE U.S.A.:									
Atlantis II st. 100	37 + (?*c.* 65)	11·5	–	10	0·95	93	6	2	0·92
Syntypes of	68 + (?*c.* 80)	14·5	*c.* 5·5	10,11	0·92	96	6	3	0·83
Pontaster	60 + (?*c.* 75)	14	–	15	1·00	104	5	4	–
forcipatus	37 + (?*c.* 65)	13·5	–	13	0·71	83	5 (6)	3,4	0·92
	57 + (?*c.* 65)	12	*c.* 5·4	10	1·00	109	6	4,5	1·1
	50	11	4·5	9	–	65	7	2	–
Gulf of Guinea:									
Pillsbury st. 34	–	13	–	21	0·75	80	7	2	0·9
Pillsbury st. 34	–	12·5	–	23	–	60	8	2 (3)	–
Pillsbury st. 34	–	13	–	17	–	82	7	3	–
South Africa:									
[No data] Gilchrist	50 + (?*c.* 62)	10·5	*c.* 5·9	13	1·08	82	6 (7)	4	0·83
[No data] Gilchrist	72	14	5·1	*c.* 15	1·17	89	8	2,3	1·05
Crozet Is area:									
Syntypes of *Pontaster*	60 + (?*c.* 80)	14·5	–	17,18	1·25	100	6 (7)	5	1·00
forcipatus var.	73 + (?*c.* 82)	14	*c.* 5·9	15	1·17	115	6	4	1·17
echinata	40 + (?*c.* 55)	11·5	–	10	0·92	95	6	3	–
	52	9·5	5·5	9	0·83	76	6	2	–

specimens from the NE Atlantic but this may not be significant since the latter are mostly smaller.

As for *Pontaster pristinus* Sladen, based on a single small specimen from *Challenger* st. 325, off the River Plate, this is clearly a *Pectinaster* sensu stricto, having relatively narrow superomarginals in dorsal view and compact, slightly bulging, papularia. Reexamination of the holotype throws considerable doubt on Sladen's arguments about its distinction from *P. forcipatus*. The specimen was coated with fine mud. When this was removed, the abactinal plates of the disc were found to have clusters of up to 7 spinules, usually 4 or 5, around the fine spinelets, the tips of which were seen by Sladen, the armament being in fact indistinguishable from that of specimens of *P. filholi* of similar size (e.g. from *Challenger* st. 46, R *c.* 18 mm). (Sladen somehow misjudged R in *pristinus* as only 11·5 mm but the complete arm remaining, though curled over, is at least 5 mm longer than this. Only two pores could be found in the papularium cleared and the abactinal spinelets of the disc are up to 0·6 mm long. The condition of the arm plates is poor but does not appear to be significantly different from small specimens of *P. filholi* and the madreporite is no more conspicuous than can be attributed to adpression of the armament in its vicinity. There are 4 or 5 furrow spines on the proximal adambulacral plates with a few similar spines in series with them proximal and distal to the large conical subambulacral spine. Three North American specimens with R 18–21 mm, have 3, 4 or 6 pores in one papularium but this is probably not significant in view of the variation in pore number shown by other specimens of *filholi*. Nor do I consider the absence of pedicellariae in the single specimen of *P. pristinus* justifies a specific distinction, though pedicellariae are more or less numerous in most specimens from the NW and NE Atlantic examined.

Outside the Atlantic, *Pectinaster* includes *P. agassizi* (Ludwig, 1905) from the East Pacific and *P. mimicus* (Sladen, 1889) from the Indian Ocean, East Indies and New Zealand. Despite its having enlarged spinelets on the lateral as well as midradial abactinal arm plates and only 12–14, rather than 15–18, proximal adambulacral plates matching the first ten inferomarginals, *P. hylacanthus* Fisher, 1913, from the Philippines and Indonesia, was reduced to a subspecies of *P. mimicus* by Döderlein, 1921. If these characters are of less than specific weight, then *P. hispidus* (Woodmason & Alcock, 1891) from the Indian Ocean is also conspecific with *P. mimicus*. This synonymy is supported by comparison of a paratype of *P. hispidus* with the holotype of *P. mimicus*. Further, Macan (1938) identified several specimens from the Gulf of Aden as *P. agassizi* or *P. agassizi granuliferus* subsp. nov. rather than *P. mimicus*. The new subspecies was said to differ in having abactinal central spine(let)s on the arms restricted to the midradial areas and more granuliform spinelets on the actinal plates (besides differences in the distribution of the pedicellariae—not significant in my view), these two characters being also used by Macan to differentiate *P. mimicus* from the specimens he called *P. agassizi*. The fact that his largest specimens from the Gulf of Aden have R 119 and 158 mm could well account for the very high number of 40–50 pores in the papularia in apparent agreement with *P. agassizi* compared with up to only 20 in the few specimens attributed to *P. mimicus* in which pores have been counted (the types of *P. mimicus* with R 78 mm and of *P. mimicus palawanensis*, R *c.* 95 mm), both Fisher and Döderlein having apparently given little weight to relative pore number as taxonomically significant in *Pectinaster*. East Pacific material of *P. agassizi* has even more numerous pores—already *c.* 55 at R only 65 mm from *c.* 25 at R 45 mm, so that the number is likely to be even greater when (if) R exceeds 100 mm.

Of the other nominal species included in Macan's table for *Pectinaster, Pontaster cribellum* Alcock, 1893, was compared by Alcock rather with *P. subtuberculatus* Sladen, since referred to *Cheiraster*. Alcock's holotype had R only 45 mm and this could account for the still rounded rather than bilobed form of the papular areas. Finally, *Pectinaster robustus* A. H. Clark, 1917, from off Chile, has two large subambulacral spines and reexamination of the large holotype showed the pore areas (Fig. 5d) to be deeply bilobed distally and not restricted to specialized papularia. *P. robustus* is therefore now referred to the subgenus *Luidiaster* of *Cheiraster*. This action brings *robustus* into conflict as a junior secondary

Table 7 Data for the *Pillsbury* specimens of *Benthopecten.* For the abactinal spinules per proximal plate '1+' signifies an enlarged spinelet or spine on some plates; for disc spines (which tally includes enlarged spinelets more than twice as long as the ordinary spinules), C, R and I in capitals or lower case signify large or small central, primary radial and primary interradial spines, the rest being irregular in position; for pore extent, the number is the superomarginal plate opposite the distalmost pores; the adambulacral count is of the proximal ones opposite the first 10 inferomarginals; brackets around entries signify occasional occurrence.

Pillsbury station	Abactinal spinules proximal	distal	Disc spines	Pore extent	Adambs: 10 i.m. pls	Furrow spines
681, Guyana Basin	1 + 3–10	1–6	1C,4R + *c.* 50	4	19	6–8
	1–4	1–3	1C	3	19½	5
782, Colombia	3–10	–	1c,2r + 3	3	–	*c.* 6
1178, E Cuba	2–5	1–3	0	–	–	6
120, Florida/ Bermuda	3–6	1–3	1c,2r,2i + 2	4	16 (15)	6–8
	1,2 (3)	1–4	1C,1r	2	21	*c.* 7
	1–4	1	2R + 3	1	19	*c.* 5
314, Gulf of Guinea	1 + 3–10	1	1C,2r + 8	5	21	7
	1–5	1–3	1C,2r,1i	4	21½	7–6
34, Gulf of Guinea	1 (2,3)	1	0	2–3	21½	6 (5,7)
	1 (2,3)	1 (2)	1c + 1	2	–	7 (8)
681, Guyana	1 (2)	1	1C,1R,2r, 3(? + 2)I + 3	3	16½	5,6 (7)

homonym with the species-group name *robusta* Sladen, 1889, originally described as a variety of *Pontaster venustus* but now referred to the synonymy of *Cheiraster (Cheiraster) sepitus* (Verrill, 1885). However, *robustus* (A. H. Clark) may well prove to be conspecific with *C. (L.) planeta* (Sladen, 1889), type locality off southern Chile, when specimens of intermediate size are available for comparison.

Turning to benthopectinids with odd interradial marginal plates, *Benthopecten* itself is well represented in the Atlantic and also in need of review.

BENTHOPECTEN Verrill

Benthopecten Verrill, 1884 : 218 (footnote); 1895 : 130; Ludwig, 1910 : 464–466; Fisher, 1911 : 142–144; Macan, 1938 : 351–352; Downey, 1973 : 40.

Pararchaster Sladen, 1885 : 610–611; 1889 : 4–7; Ludwig, 1910 : 462–464. (Type species, by monotypy, *P. pedicifer* Sladen, 1885).

Type species. *Benthopecten spinosus* Verrill, 1884, by monotypy.

Diagnosis. A genus of Benthopectinidae with an odd interradial marginal plate in each series, usually in all five interradii, the superomarginal one more or less inset on to the disc and bearing a conspicuous spike-like vertical spine (or occasionally a cluster of *c.* 3 small spines); abactinal plates thin, flat and scale-like, at least on the arms, but sometimes convex medially on the disc, never markedly paxilliform, each bearing one or more spinules, some of which may be elongated into spinelets or even spines more than 1·5 mm long, especially

Pillsbury	Subamb.	Oral f.	Suboral	Pedicellariae				
station	spines	spines	spines	Abact.	Act.	i.m.	R	r
681, Guyana Basin	2	5	4	(+)	+	+	100 + (?*c.* 150)	20
	2	5,4	4	(+)	+	+	40 + (?60–70)	9·5
782, Colombia	2	6	4	+	+	+	20 ++ (?70–100)	11·5
1178, E Cuba	(1)	6	2,3	—	+	+	?? v. poor	9·5
120, Florida/ Bermuda	2 (1)	7,8	5,6	+	(+)	(+)	100	11
	1 (2)	*c.* 6	4,5 (6)	(+,1)	(+,1)	+	50 + (?*c.* 70)	9
	1 (2)	5 (4)	3 (2)	—	—	—	30	6
314, Gulf of Guinea	2	6,7	3	+	+	+	75 ++ (?*c.* 130)	19
	2	6	5	+	+	+	100 + (?*c.* 150)	20
34, Gulf of Guinea	1 (2)	6	3	+	+	+	45 + (?70–80)	9·5
	1 (2)	7 (8)	4	+	+	+	30 + (?*c.* 70)	9·0
681, Guyana	2	4,5	4	—	(+,1)	—	45 ++ (?*c.* 110)	15

on the primary plates of the disc; papulae scattered on the arm bases, usually extending further distally close to the marginal plates, so the areas become bilobed, sometimes covering much of the disc and a limited distance (usually $<\frac{1}{2}$R) along the arms; marginal plates with at least one long spine, the inferomarginals usually with an accessory spine (or two) below the main one but smaller; adambulacral plates with the furrow margin rounded or angular, armed with 3–8, sometimes more, radiating, slender furrow spines backed by one or two (rarely three) larger subambulacral spines usually aligned almost at right angles to the furrow when more than one occurs but in some species nearly parallel to it; some pectinate pedicellariae usually present, especially on the actinal plates, but often also between some abactinal or inferomarginal plates, especially proximally.

REMARKS. Verrill's extraordinary omission in 1884 (though rectified in 1885*b* : 519) to mention the most obvious characteristic of *Benthopecten*—the odd interradial superomarginal plates with their conspicuous single spines—led Sladen (1885 & 1889) to refer his several species to a new nominal genus *Pararchaster.* In 1894 Verrill referred *Pararchaster* to the synonymy of *Benthopecten.* Although Ludwig (1910) tried to retain two genera on the basis of the multiple abactinal spinelets of *Pararchaster pedicifer* Sladen, the type-species of *Pararchaster,* as opposed to the single ones of *Benthopecten spinosus*, Fisher (1911) found this distinction untenable at the generic level, following observations on the more abundant North Pacific material available to him. Study of the material of *Benthopecten* collected in the deep tropical Atlantic by the *Pillsbury* raises new doubts about even the specific significance of the frequency of the abactinal armament in many cases. These new specimens yield the data included in Table 7, from which it is evident that the very small samples collected at stations as wide apart as the Gulf of Guinea off West Africa, the Guyana Basin off northern South America (outside the Antillean chain) and the North American Basin between Florida and Bermuda, show a wide range within each sample in abactinal spinule frequency. The maximum spinule number is found in one large specimen from st. 681 off Guyana and another from st. 314 in the Gulf of Guinea, each sample including a second specimen with much less dense armament but otherwise not significantly different. St. 120 also includes one more spinulose specimen out of three, though the difference is less marked. However, a third specimen was collected at st. 681; this is the single individual, segregated in Table 7, having the minimum of abactinal spinelets—rarely more than one, which may be specifically distinct. Such a conclusion is supported by its primary *interradial* disc spines appearing to be better developed than the primary radial ones, coupled with there being rarely as many as 7 furrow spines (and that only on odd plates), where 6 or 7 is the usual number in the other specimens, and only a single (actinal) pedicellaria, where all the rest with R > 50 mm have several actinal and inferomarginal pedicellariae and usually also some abactinal ones. A review of the fairly abundant material of *Benthopecten spinosus* from the eastern continental slope of the U.S.A. has shown a consistent agreement in these same characters, except that the rare pedicellariae found were only on the inferomarginal and not the actinal plates.

In comparison with other Atlantic species, a multispinulose condition with up to 10 spinules on some abactinal disc plates is shown by the four syntypes of *B. spinosissimus* (Sladen) from off Ascension I (R 60–68 mm) and the holotype of *B. fischeri* (Perrier) from NW Africa (R *c.* 40 mm), the latter reexamined at the Paris Museum.

In *B. spinosissimus* already at R < 70 mm the papulae extend distally to level with the sixth or seventh superomarginals and the marginals themselves are relatively short and numerous, numbering 47–53 in each series in the syntypes, giving a ratio of 1·2–1·4/1 for R/SM number. This compares with only about 30 marginals and a ratio of *c.* 2·2/1 at this size in *B. spinosus* and probably a similar number in *B. simplex* (Perrier), of which a specimen with an intact arm showing R 55 mm has only 25 superomarginals, also giving a ratio of 2·2/1. A further distinction of *B. spinosissimus* is the small number of furrow spines, only 3 or 4 on each plate, leaving little doubt of its specific distinction.

With regard to *B. fischeri*, I found the holotype and only recorded specimen to have 4 or 5 spinules on most proximal abactinal plates but additional ones on some plates with an enlarged spinelet or spine, apparently an unusually high frequency at this relatively small size. Although the jaws have a relatively rich armament of *c.* 10 furrow spines and up to 12 suboral spines and spinelets on each oral plate, there are only 6 furrow spines on most adambulacral plates and the other characters agree with the bulk of the *Pillsbury* material. (The exception is the single *Pillsbury* specimen allied with *B. spinosus,* which is quite distinct in its very sparse armament.) *B. fischeri* was referred to the synonymy of *B. spinosus* by Grieg (1921 & 1932) on its superficial resemblance.

Grieg also followed Verrill (1895) in synonymizing *Pararchaster armatus* Sladen, 1889 with *B. spinosus*, though Farran (1913) and Mortensen (1927) maintained *armatus* as a distinct species. Ludwig (1910) had instead referred *armatus* to the synonymy of *Archaster simplex* Perrier, 1881, the oldest name for any species of *Benthopecten.* The holotype (from the Gulf of Mexico NW of Cuba) has R only 18 mm and, until the *Oregon* and *Alaminos* took some rather larger specimens (R 48+ mm) in the Gulf of Mexico (described by Downey in 1973), little comparative information was available about *B. simplex.* Reexamination of these specimens and comparison with the type material of *B. armatus* from S and E of Cape Cod and various specimens from the vicinity of Portugal, SW Ireland and the Rockall Trough in the NE Atlantic reveals no differences which I consider to be significant (see Table 10). The abactinal armament is multiple in all except immature specimens (numbering usually 1–5 spinules on the proximal plates), the disc spines (when developed) tend to enlarge first on the primary radial more than the interradial plates, the number of furrow spines averages 6 or 7 on most of the adambulacral plate series and the number of subambulacral spines tends to increase from one to two with size, with occasional exceptions; lastly there is a relatively high incidence of pedicellariae, often in all three loci, in all but the smaller specimens (R <40 mm), again with some individual variation.

The origin of some of the *Pillsbury* specimens from areas geographically adjacent to the Gulf of Mexico (the nearest being from st. 1178 east of Cuba) and their morphological resemblance to the rather smaller and mostly less well preserved *Oregon* and *Alaminos* specimens reinforces belief that all can be referred to *B. simplex* but for the exceptional specimen from st. 681 which is indistinguishable from *B. spinosus*. This serves both to extend the known size range of *B. simplex* to R *c.* 150 mm and also to extend the geographical range (not unexpectedly in view of the great depths) not only to both sides of the North Atlantic but also both sides of the tropical Atlantic, including the Gulf of Guinea, taking in the type locality of *Benthopecten chardyi* Sibuet, 1975. Despite several peculiarities of Sibuet's unique holotype (discussed further below), it seems to fall within the range of variation of *B. simplex*.

CHARACTERS. Apart from the density of the abactinal armament (now considered to be of only limited use) the following characters have been adopted as of some taxonomic significance in distinguishing the species of *Benthopecten*:

1. The development of enlarged spines on the centre of the disc (by Ludwig)
2. The relative size of any accessory spines on the inferomarginal plates (Sladen, Ludwig and Fisher)
3. The number of paired marginal plates in each series (Sladen)
4. The numbers of furrow and subambulacral spines (Sladen *et al.*)
5. The number of oral furrow spines (Ludwig)
6. The number of adambulacral plates corresponding to the first ten paired inferomarginal plates (Ludwig and Macan, 1938)
7. The occurrence of pedicellariae (Sladen *et al.*)
8. The presence of more than one superomarginal spine (Sladen and Macan)
9. The substitution of several small spines for the usual conspicuous odd interradial superomarginal spine (Perrier, 1894, for *B. folini*)
10. The extent of papulae along the arm (Fisher and Macan)
11. The extent of the inferomarginal pedicellariae along the arm (Fisher and Macan)
12. The number of actinal pedicellariae (Macan)

Other characters which can be considered as possibly significant for some of the species but needing further comparisons for appreciation of their wider significance within the whole genus are:

13. The occasional non-bifurcation of the papular areas distally
14. The relative size of the primary radial and interradial disc spines, when developed
15. The number of suboral spines
16. The presence of more than one series of actinal plates and
17. The relative size of the first paired superomarginal spines.

Fortunately, since the arms are rarely preserved intact, the R/r ratio does not appear to be taxonomically significant in this genus, the relative disc size being apparently variable over a similar range in all the species. As in many long-armed asteroids, the R/r ratio tends to increase allometrically with absolute size.

As with the characters based on the abundance of abactinal spinules, most of the others are subject to some degree of variation.

No. 1, the development of enlarged spines on the disc, depends to some extent on size and is also subject to variation. For instance, in large specimens of *B. spinosus*, R >90 mm, the disc spines range from few and inconspicuous, <1·5 mm long, to a cluster of 20 or more, some exceeding 6 mm in length. An elaboration of this is character no. 14, the relative size of the primary radial and interradial disc spines, when developed, studied now only in *B. spinosus* and *B. simplex*, where a range of specimens is available. As detailed under the heading of *B. simplex*, on average the primary radial spines in that species are equal to or slightly larger than the primary interradial ones, whereas in *B. spinosus* the interradial spines are mostly better developed (not counting those of the madreporic interradius where the spine development is generally erratic). This character remains to be evaluated in other species.

No. 2, the mean size of the accessory inferomarginal spine (if developed) relative to the main spine above it, appears to be somewhat variable and is of uncertain value because of paucity of information about its range, only holotypes having often been described. In some species such as *B. spinosus* it seems to be fairly consistently at least half as long as the main spine, whereas in *B. simplex* the reverse is true and it rarely exceeds half the spine length. (An exception again is the holotype of *B. chardyi* where the accessory spine is often large and may even equal the main spine on some plates.) Very spinose species such as *B. spinosissimus* have several successive accessory spines on each plate, graduating in size.

No. 3, the number of marginals relative to R, remains to be investigated for most species, marginal counts having rarely been cited by authors, partly because so few specimens are usually obtained with any arms intact. The development of additional marginal plates adjacent to the terminal does not keep pace with the elongation of the arms so that the ratio of R/SM number tends to increase with R. In 12 specimens of *B. spinosus* with R 35–155 mm, the ratio ranges from 1·8/1 (in the smallest) to 3·4/1 (in the largest), whereas nine specimens with R 70–110 mm have a range of 2·3–3·0/1 and a mean of 2·6/1. The holotype of the closely related *B. semisquamatus* (Sladen), from Japan, does not differ significantly, having a ratio of 3·0/1 at R 166 mm. In contrast, as mentioned above, the four syntypes of *B. spinosissimus* with R 60–68 mm have a ratio of only 1·2–1·4/1, the marginals being relatively short and more numerous, 47–53, as opposed to only 32 in a specimen of *B. spinosus* with R 73 mm.

No. 4, the numbers of furrow and subambulacral spines, may show a wide range along the furrow length of a single specimen, usually tending to increase beyond the proximal plates and to a greater extent in very large specimens. For instance, in the holotype of *B. heteracanthus* Macan from the Indian Ocean, R 210 mm, the number increases from 7 or 8 proximally to 11 on many distal plates, while the holotype of *B. polyctenius* Fisher from Indonesia, at R 224 mm, has a range from 9–14. Two smaller specimens of *B. polyctenius* with R 120 and 80 mm have lower maxima of 11 and 9 respectively. In species of more restricted size range, the range in furrow spine number is probably restricted to *c.* 3 or 4. For instance, in *B. spinosus*, known to reach R 155 mm, the range is 4–6, predominantly 5, even in larger specimens, R >90 mm, while *B. simplex* with a similar size range usually has 6 or 7, occasionally 5 or 8 spines. The holotype of *B. chardyi* Sibuet (now thought to be less than specifically distinct from *B. simplex*) has 5 or even 4 spines on about the first ten adambulacral plates but the number increases first to 6 then 7 beyond about the twentieth plate. As for the subambulacral spine number, up to a size of R 30 mm *B. simplex* has only single spines on nearly all the plates, then in most specimens a second spine becomes enlarged beyond the most proximal plates so that specimens with R >60 mm usually have two subambulacrals predominating throughout the series. (The holotype of *B. chardyi* with single spines on most plates could be interpreted as neotenous in this respect; two slightly smaller specimens of *B. simplex* also from the Gulf of Guinea have a small second spine on some plates.)

No. 5, the number of oral furrow spines, would be expected to vary through the same sort of range as the mean number of adambulacral furrow spines. Certainly *B. polyctenius* shows a range of 8–14 according to Fisher (1919). *B. spinosus* has 5 or 6, occasionally 4, and *B. simplex* shows a range from 5 to 8, compared with 10 (or even 11) oral furrow spines in the holotype and only mature specimen of *B. fischeri* (Perrier) at R only *c.* 40 mm, which in other respects resembles the more spinulose specimens of *B. simplex* and has only *c.* 6 furrow spines on the adambulacral plates. Until more material from the type locality of *B. fischeri* is available, the significance of this character remains to be determined.

No. 6, the number of adambulacral plates relative to the first ten paired inferomarginals, appears to vary over a range of 4 or 5, sometimes more, in a single species (see Tables 9, 10), judging from the data available. Unfortunately, even Ludwig, who initiated its use, failed to cite it for several species and not all subsequent authors have included counts in their descriptions. The usual number in *B. spinosus* is 17–20, while in *B. simplex* between 18 and 21 is common but as many as 24 (or even 25) are found, for instance in the anomalous holotype of *B. chardyi.* Also in the holotype of *B. violaceus* (Alcock) from the Indian Ocean 24 are supposedly found but this number is derived only from the drawing, not Alcock's description, and may not be correct.

Nos 7, 11 and 12. The occurrence and frequency of pedicellariae are notoriously variable and rarely reliable in diagnosing most asteroid species; this is equally true of *Benthopecten.* Only a large sample (rarely provided) can give a good idea of the relative frequencies of abactinal, actinal and inferomarginal pedicellariae. Even in *B. spinosus*, in which pedicellariae have long been thought to be consistently rare or absent, an additional sample of ten specimens from the *Atlantis II* collections showed four with at least some inferomarginal pedicellariae.

No. 8, the presence of accessory superomarginal spines in species such as *B. spinosissimus* is correlated with a generally higher frequency of spines on all the plates and is not in itself significant.

No. 9, the absence of conspicuous spines from the odd interradial superomarginal plates, as described in *B. folini* (Perrier, 1894), from off NW Africa, is not shown by all specimens of the type series so one must conclude that either two sympatric species were included or that the character is variable. If there are two species in the type series, the one with multiple diminutive spines on the odd plates also usually has two subambulacral spines. The other, with single large spines may have one subambulacral spine and is then indistinguishable from *B. simplex chardyi.* It is not certain which specimen in the Paris Museum collections Perrier used for his full description; the arms were broken and he could only cite r, which he gave as 12 mm. The largest specimen from off Cap Blanc (*Talisman* 1883 haul 96, P.M. no. 3304) is almost certainly the one shown in Perrier's pl. 19, figs 1a and 1b of a general view, above and below; I estimate its r as 10·0–10·5 mm (some shrinkage during nearly 100 years in spirit is not unlikely); R is 65 + ?10–20 mm; all the odd superomarginals have small spines and there are two subequal subambulacral spines on most plates. Of the two specimens from haul 98, slightly further south (P.M. nos 3317 and 3318) one has had the abactinal body wall removed and is the specimen so mutilated shown in Perrier's pl. 20, fig. 1c. The second has R50 + ?20–30 mm, r *c.* 11 mm and so could be the specimen from which pl. 20, figs 1a and 1b of details of parts of the disc were made, though there are some divergencies between the finer details of armament and Perrier's description. Accordingly, the largest specimen from off Cap Blanc is now designated as lectotype; its subambulacral armament was probably misrepresented as single in pl. 19, fig. 1a by Perrier's artist. However, of the four (not three) smaller and more broken specimens from this same haul 96, one has relatively large single odd superomarginal spines up to 6 mm long, R being 20 + ?*c.* 30 mm; its subambulacral spines are mostly single. The other three are more damaged interradially, the spines of the odd plates mostly lost; one has a pair of large spines still attached to one plate and signs of paired spines in at least two other interradii. From *Talisman* haul 97 (no. 3305) come three more damaged paratypes, at least one with three massive single odd superomarginal spines.

Possibly these large spines are vulnerable to damage or loss from the attacks of predators and the anomalies in development are due to differential regeneration. In the holotype of *B. pikei* H. E. S. Clark, 1969, from New Zealand, in four out of five interradii the spines are relatively small and in 1970 she suggested that this might be attributable to injury when she described a variety *australis* of *B. pikei* from two specimens with all the odd spines large.

No. 10, the distal extent of the papulae along the arms, progresses during growth, usually from level with the first superomarginal to the third or fourth, while the distalmost pores are usually lateral rather than midradial (character no. 13). However, in *B. acanthonotus* Fisher, from off California, the distal extremity varies in three large specimens from level with the fifth superomarginal to the twentieth. In this species the papular areas are consistently bifurcating but the holotype and only described specimen of *B. indicus* Koehler, from off Sri

Table 8 Tabular key to the species of *Benthopecten* known from the Atlantic.

Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
spinosus	1 (2)	+ I	S	3,4	L	$\frac{1}{2}$–$\frac{2}{3}$	16$\frac{1}{2}$–20	4,5 (6)	2	5 (6)	3,4 (5)	—	—	(+)	155
simplex chardyi	1 (2–4)	—	S	3	L	$\frac{3}{4}$	24–25	(4) 5–7	1	(5) 6,7	3,4	+	+	+	90–100
simplex simplex	1–5/ + 3–10	+/(+)R	S	2–5	L	$\frac{1}{4}$–$\frac{1}{3}$	16–23	6,7	1,2	5,6	3,4	(+)	+	+	*c.* 150
folini	1 (2,3)	(+)	S	4	Sm	*c.* $\frac{1}{2}$	?*c.* 20	7 (8,9)	2 (1)	7	4	+	+	+	75–80
fischeri	1 + 3–10	(+)	M	4	L	*c.* $\frac{1}{2}$	20–21	*c.* 6	2	10 (11)	*c.* 12	—	+	+	39
spinosissimus	1 + 2–10	(+)	M	6,7	L	$\frac{2}{3}$–$\frac{3}{4}$	19–23	3 (4)	2	8	3,4 (+ 2)	—	+	(+)	70

Tables 8 and 9 Tabular keys to the Atlantic and non-Atlantic species of *Benthopecten*.

1. Armament of most proximal abactinal plates: simple numbers indicate the number of spinules; 1+ signifies an enlarged spinelet or spine in addition to some spinules; () signifies occasional numbers
2. Occurrence of central disc spines > 1·5 mm long: + well developed, > 10; (+) inconspicuous, *c.* 5; — lacking (except sometimes for a single anal spine); I primary interradial ones larger; R primary radial ones larger
3. Number of spinules on abactinal arm plates beyond papular areas: S single; M multiple
4. Superomarginal opposite distalmost papular pores
5. Size of odd superomarginal spine: S small; M moderate; L large; m multiple (otherwise single)
6. Length of accessory inferomarginal spine relative to that of the main spine
7. Number of adambulacral plates corresponding to the first 10 paired inferomarginals
8. Number of furrow spines
9. Number of subambulacral spines
10. Number of oral furrow spines
11. Number of suboral spines
12. Occurrence of abactinal pedicellariae: (+) signifies rare; ++ very numerous
13. Occurrence of actinal pedicellariae
14. Occurrence of inferomarginal pedicellariae
15. Maximum R of specimens recorded or now studied

Table 9 Tabular key to the non-Atlantic species of *Benthopecten*.

Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	General area
semisquamatus	1	+	S	4	L	$\frac{3}{4}$–$\frac{7}{8}$	16	4–5	2	4–5	3	–	–	–	166	Japan
*huddlestoni**	1	+	S	4	L	?	?17	6–8	2$\frac{1}{2}$	6–7	3	–	+	+	*c.* 170	Indian Ocean
moluccanus	1	+	S	3	L	*c.* $\frac{7}{8}$	19,20	7–9	2	5–8	3–5	++	+/–	+	80	East Indies
pikei	1(–4)	+	M?	4,5	M	'shorter'	?	5–8	2 (3)	5–7	7–10	–	+	(+)	*c.* 80	New Zealand
pectinifer	1	(+)	S	5	L	?	18	5,6 (7)	2	6–8	4,5	+	+	+	160+	East Pacific
heteracanthus	1(–4)	(+)	S	6	L	$\frac{1}{2}$–$\frac{2}{3}$	17–18	7–11	2	6	3	–	+	+	210	Indian Ocean
pedicifer	1–4	(+) R	M	4	M	$\frac{2}{3}$	17,19	(6) 7,8	3 (2)	7 (6)	6,7	++	+	+	168	Southern "
styracius	1–3	(+)	M	3	L	$\frac{1}{2}$–$\frac{3}{4}$	19–22	7,8	2 (+$\frac{1}{2}$)	6	3	++	+	+	105	Philippines
incertus	1 (2,3)	–	?	?	?L	0	?	4	2	4,5	?	–	–	–	'young'	Indian Ocean
*violaceus**	2–4	–	M	2	L	*c.* $\frac{1}{2}$	?24,25	7,8	2	7,8	2	–	–	(+)	*c.* 100	Indian Ocean
pikei v. *australis*	3–6	+	M	?	L	?	?	6	2	4,5	?	?–	(+)	+	150	New Zealand
cognatus†	2–4(–12)	(+)	M	5	L	0	15,16	6 (5)	2	6	?	++	(+)	+	160	East Pacific
indicus	1 or 6–10	+	M	12	L	?	?	3	2	?	?	+	+	–	*c.* 120	Indian Ocean
claviger	1 + 8–15	+	M	5,6	M–L	*c.* $\frac{7}{8}$	19	4–6	2	5,6	6	+	+	+	110	North Pacific
acanthonotus	1 + 1–6	+ (+)	S	5–20	L	$\frac{1}{2}$–$\frac{2}{3}$	?	4,5 (–7)	2	4,5	4,5	+ (+)	+ (+)	(+)	164+	East Pacific
rhopalophorus	1 + ?5–9	+	M	5,6	L	?*c.* $\frac{7}{8}$	?	5–7	2	?	?	–	(+)	–	130	N-w Pacific
munidae	1 + 2–5	'small'	M	7,8	L	?	?	5–7	2	11,12	4,5	–	+	–	45	New Zealand
spinuliger†	1 + 3–12	(+)	M	3	L	?$\frac{1}{2}$	20	5 (4)	1 (2)	13–15	3–5	(+)	+	+	75	East Pacific
polyctenius	1 + 10+	(+)	M	4	Mm	'shorter'	20	8–14	2 (+ $\frac{1}{2}$)	7,8	3–5	++	+	++	225	East Indies

**B. huddlestoni* and *B. violaceus*: the entry in column 6 depends on the accuracy of the artist of the *Investigator* illustrations.

†*B. cognatus* and *B. spinuliger*: the entries in column 1 (and 3 for *cognatus*) are based on re-examination of the type material.

B. pentacanthus Fell, 1958, is omitted since the holotype had R only 5 mm and could only show juvenile characters common to most of the species.

Lanka (R *c.* 120 mm) has the papulae extending to superomarginal 12 for the whole width of the arm. In a *Pillsbury* specimen from NE of Florida (R 100 mm), now referred to *B. simplex*, the papulae extend to the fourth superomarginals and the areas do not bifurcate. Also in the holotype of *B. chardyi* the distalmost pores are adradial rather than abradial and extend only to the third superomarginal though R is 90–100 mm. However, two slightly smaller *Pillsbury* specimens also from the Gulf of Guinea have the areas bifurcating; their papulae extend distally to the third (or even the distal ends of the second) superomarginals. Isolated cases of non-bifurcating areas have been recorded from at least one non-Atlantic species and proper scrutiny of more material may well show occasional instances of this, suggesting that character 13 has little taxonomic significance. Since in some benthopectinids the dorsal arm muscles are attached at least partially to the dorsal body wall near the base of the arm, as well as or rather than to the ambulacrals and marginals, this might have a limiting effect on the extent of the pores medially.

No. 15, the number of suboral spines, is usually 3 or 4 (sometimes 5) on each plate in most species, accompanying spinelets being rare. Occasionally higher numbers are found. Reexamination of the holotype of *B. fischeri* from NW Africa showed a total of *c.* 12 suboral spines and spinelets on each plate, four of them distinctly larger than the furrow spines. In contrast, the four similarly multispinose syntypes of *B. spinosissimus* from near Ascension Island have only 4 suboral spines on most plates, though there may be one or two additional spinelets on some plates. The oral furrow spines on the type of *B. fischeri* are also unusually numerous, as discussed under character 5.

No. 16, the number of series of actinal plates, is correlated with the relative disc size, as well as tending to increase with growth. Until an R of *c.* 100 mm, rarely more than one series is well developed. More larger specimens are needed to evaluate this character.

No. 17, the relative size of the first paired superomarginal spines, shows a considerable range from very reduced in comparison with the fourth (usually the largest) spine to almost as large as the odd interradial spine. It can result in very different appearances of the interradii but preliminary observations suggest that it is too variable (even within one specimen) to be significant.

The characters thought to be most useful are utilized in two tabular keys (Tables 8 and 9) to distinguish the Atlantic and non-Atlantic species of *Benthopecten*. Analysis of these tables shows only very minor differences in variable or largely untested characters between several of the nominal species or differences possibly attributable to growth changes; notably *B. spinosus* Verrill and *B. semisquamatus* (Sladen) are separated only by an insignificant difference in the number of adambulacrals relative to the inferomarginals. The occasional presence of inferomarginal pedicellariae in *B. spinosus* may well prove to be shared by some specimens of *B. semisquamatus* other than the syntypes, when more material is available for comparison. This close affinity was observed by Sladen, who treated an east American specimen, now regarded as conspecific with *B. spinosus*, as only a variety *occidentalis* of *B. semisquamatus*. Inter-oceanic distributions of abyssal species such as these are very likely. If the present decision to treat Atlantic specimens showing a considerable range of variation in density of the abactinal armament as a single species, *B. simplex*, is proved correct, then barriers to the conspecificity of many nominal species in the middle and lower parts of Table 9 will be almost completely broken down and there should be a drastic reduction in the number of valid species of *Benthopecten* recognized.

Since *Benthopecten simplex* is the first-named species of the genus and its limits—both morphological and geographical—are considerably extended by the *Pillsbury* and other specimens now considered to be referable to it, a full account of this species is given here.

Benthopecten simplex (Perrier)

Archaster simplex Perrier, 1881 : 28; 1884 : 264, pl. 1, fig. 8.
Pararchaster armatus Sladen, 1889 : 19–22, pl. 1, figs 5, 6, pl. 4, figs 5, 6.
Pararchaster simplex: Perrier, 1894 : 253, 254–256.

'*Pararchaster* nov. sp. (*P. Fischeri* Perrier aff.)' Mortensen *in* Schmidt, 1904 : 24.

Benthopecten simplex: Ludwig, 1910 : 461, 464, 465, 466; Fisher, 1911 : 143; Verrill, 1915 : 1·22; Downey, 1973 : 40, pl. 12, figs C, D.

Benthopecten armatus: Farran, 1913 : 2–3; Mortensen, 1927 : 74–75, fig. 41.

Benthopecten spinosus (pt) Grieg, 1921 (& 1932) : 12–13, pl. 4, fig. 1 (*Michael Sars* sts 95 & 101 at least); H. L. Clark, 1941 : 26. (Non *B. spinosus* Verrill, 1884).

Benthopecten chardyi Sibuet, 1975 : 283, 289–291, fig. 3, pl. 1, figs B, D

R is probably up to *c.* 150 mm but rarely more than 80 mm; R/r is 7·7–7·9/1 and R/no. of superomarginal plates *c.* 2·25/1 in three specimens with R 50–55 mm.

DIAGNOSIS. A species of *Benthopecten* with multiple spinules on most proximal abactinal plates, often 2 or 3 but sometimes up to *c.* 10 when they are accompanied by a larger spinelet or spine, especially at R > *c.* 50 mm, those on the primary radial plates tending to be better developed than those of the primary interradial plates; papular areas usually distally bifurcate, the distalmost pores level with the second or third superomarginals in specimens with R 50–80 mm but extending to the fourth or even the fifth in those with R > 100 mm; odd interradial superomarginal plates with a single very large spine, other superomarginals also with single spines and a few small spinelets or spinules, inferomarginals with an accessory spine below the main one but usually less than half as long; 16–23, usually 18–21 proximal adambulacral plates corresponding to the first ten paired inferomarginals (though up to 25 in the holotype of *B. chardyi*); actinal plates few, a second series only developed at R > 100 mm; adambulacral plates with 6 or 7 furrow spines (sometimes 5 or 8) and one or two subambulacral spines, usually two at R > 50 mm beyond the first ten or so plates, where there is more often only a single spine; oral plates with 5 or 6 (sometimes 4 or 7) furrow spines and 3 or 4 (5) suboral spines; actinal and some inferomarginal pedicellariae usually present at R > 50 mm and sometimes also some abactinal ones.

VARIATIONS. As mentioned under the generic heading, the armament of the abactinal plates is very variable in *B. simplex,* if I am right to include most of the *Pillsbury* specimens. At R 50–70 mm there are usually 2 or 3 (1–5) spinules on the proximal plates and single ones on the plates distal to the pore areas but occasional specimens of this size and larger ones may have some proximal plates enlarged with a bigger spinelet and up to 10 spinules.

The degree of enlargement of spinelets and spines is also variable. Even at R *c.* 70 mm there may be only a single central spine appreciably larger than the spinules, though usually several others may exceed 1·5 mm in length at this body size, especially on some of the primary plates.

The papular areas normally bifurcate distally but the largest specimen from *Pillsbury* st. 120, NE of Florida, has the distalmost pores adradial.

The odd interradial superomarginal spines are usually very conspicuous but on occasional specimens one or more of them may be reduced in size.

The length of the accessory inferomarginal spine is usually less than half that of the main spine but it may be lacking altogether on most plates of a few individuals or conversely be nearly equal in length to the main spine on some plates, e.g. of the paratype of *Pararchaster armatus* with R 42 mm from *Challenger* st. 46—but not in the larger paratype from the same station.

In larger specimens the single subambulacral spines of the proximal adambulacral plates often give way to two spines beyond, as in Downey's specimens from the Gulf of Mexico, shown by reexamination.

Other variants are mentioned in the diagnosis.

SYNONYMY. Until Downey (1973) described some *Oregon* and *Alaminos* specimens of *B. simplex* from the Gulf of Mexico, only the juvenile holotype (R 18 mm) had been described from the West Indian area and it was difficult to establish whether Sladen's type material of *Pararchaster armatus* from SE and E of Cape Cod (*c.* 42° N, 63° W and 40° N, 66° W) is synonymous with *B. simplex*, as proposed by Ludwig (1910) or with *B. spinosus* Verrill, also

Table 10 *Benthopecten simplex* (Perrier) and a comparable specimen of *B. spinosus* Verrill. Disc spine abbreviations as in Table 7. Specimen 19 is included for comparison with Perrier's description of the holotype. *Sarsia* st. 7627 is in the southern Bay of Biscay.

Specimen and station	Proximal abactinal spinelets	Disc spines	Adambs: 10 first i.m. plates	Furrow spines	Subamb. spines	Oral furrow spines	Pedicellariae Abact.	Pedicellariae Act.	Pedicellariae i.m.	R (mm)	r (mm)
(1) *Oregon* st. 2574	2,3 (1–5)	1C,2R,1I + 10	18	7 (8)	2	6	–	+	(+)	*c.* 80	11·5
(2) *Oregon* st. 2574	1–3	1C,3R,1i + 7	–	6	2	5,6	–	+	–	*c.* 80	11·0
(3) *Oregon* st. 2574	3,4 (5)	1C,2R,1I + 3	–	7	2	6	–	+	+	*c.* 70	10·0
(4) *Oregon* st. 2574	1–5	1C + 1	–	6	1,2	5	–	+	–	–	9·0
(5) *Challenger* st. 46	2,3 (1–5)	3R + 4	20	7,8	1	6	(+)	+	–	*c.* 70	8·5
(6) *Alaminos* st. 46	1–5	1C,4R,4I + 5	20	6 (7)	1,2	5	–	(+)	–	*c.* 70	8·0
(7) *Alaminos* st. 46	1 (2,3)	1C,2R,2I	–	7	?	–	–	+	++	–	8·0
(8) *Oregon* st. 2574	1 (2,3)	2	21	6 (5)	1	5	–	–	–	*c.* 65	7·0
(9) *Challenger* st. 46	1 (2–4)	4	18	4,5	1 (2)	6	–	+	–	45	8·0
(10) *Alaminos* st. 4	1 (2,3)	1C,1R,1r + 1	19	7	2	5	–	–	+	55	7·0
(11) *Alaminos* st. 4	2 (1–3)	1C,2R,2I + 4	19	7 (6) 9	1,2	?	(+)	+	+	45	7·0
(12) *Alaminos* st. 4	1,2 (3)	1C,3R,1I	20,21	6 (5)	1 (2)	5	–	+	+	50	6·5
(13) *Alaminos* st. 4	1 (2)	1C,1R,1I + 8	19	6 (5)	2 (1)	4	(+)	+	++	50	6·5
(14) Rockall Trough	2,3 (1–5)	1c	20	7 (6)	1	6 (5)	–	++	–	*c.* 50	8·0*
(15) *Challenger* st. 50	1 (–5)	1c	20	6	1	5	(+)	+	–	37	6·5
(16) SW Ireland	2,3 (1–5)	0	23	5	1	6	–	–	–	40	6·0
(17) *Alaminos* st. 4	1 (2,3)	1c	–	?	1,2	4 (5)	–	(+)	–	35	6·0
(18) *Sarsia* st. 7627	1,2 (3,4)	1C,1R	18½	5	1	5	(+)	–	–	33	6·5
(19) *Alaminos* st. 4	1 (2,3)	–	–	3,4	1,2	4	–	–	–	16	3·5
(20) HOLOTYPE	1?	–	–	4,5	1	–	–	–	–	18	3·4
B. spinosus											
Albatross st. 2221	1	3r,4I	20	4 (3,5)	2	5,6	–	–	–	55	8·0

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*This specimen has only four rays.

from the eastern U.S.A., as proposed by Verrill (1895). Comparison of the larger specimens of Downey and Sladen, together with a few further individuals from the NE Atlantic (off Portugal, the Bay of Biscay, SW Ireland and the Rockall Trough) yields the data shown in Table 10, which also includes for comparison the only available specimen of *B. spinosus* of comparable size. Table 7 of the *Pillsbury* specimens, all but one now referred to *B. simplex,* should also be consulted.

Although the positions of the disc spines and enlarged spinelets are often irregular (especially adjoining the madreporic interradius), the contrast in the specimen of *B. spinosus* in Table 10 of four relatively large primary interradial spines with the three smaller primary radial spines (reflected also by most large specimens of *B. spinosus*) is very marked, as well as the absence of multiple abactinal spinules. Further, the presence of only 4 furrow spines on most adambulacral plates, as compared with the usual 6 or 7 of *B. simplex,* and the total absence of pedicellariae, combine to justify treating *B. simplex* as distinct from *B. spinosus* in my view and at the same time synonymizing *B. armatus* with *B. simplex*. In fact, two smaller american paratypes of *P. armatus* (R *c.* 40 and 30 mm) and the portuguese paratype (R *c.* 32 mm) do have only 5 or sometimes 4 furrow spines but this is to be expected at this size and is probably only transitory. Also occasional larger specimens of *B. simplex* lack pedicellariae and conversely a few specimens of *B. spinosus* do have some inferomarginal ones.

With regard to the relationship of *B. chardyi* Sibuet with *B. simplex*, Sibuet had only a single specimen, from the Gulf of Guinea off Gabon (*Jean Charcot* st. CY 19, *c.* 2½° S, 8° E, 2584 m.), R90–100 mm, which has been reexamined. It has only a few inconspicuous spinelets enlarged near the anus, no disc spines, the papular areas do not bifurcate distally (not observed by Sibuet), the accessory inferomarginal spines are relatively large, sometimes almost equal in length to the main spine, there are as many as 24 or 25 adambulacrals corresponding to the first ten inferomarginals (not noted by Sibuet) and the subambulacral spines are almost without exception single; the furrow spines number 6 or 7 on most plates—as usual in *B. simplex*—the 4 or 5 recorded by Sibuet being limited to some of the proximal plates and transitional to the higher numbers. Apart from the last, the combination of these characters has not otherwise been found in *B. simplex* but each of them individually is liable to vary. Two (poorly preserved) specimens also from the Gulf of Guinea but to the NW off Ghana (*Pillsbury* st. 34, *c.* 4° N, 2½° W, *c.* 1970 m) with R *c.* 70 mm have a majority of the adambulacral plates with one rather than two subambulacral spines. However, one of them has two small disc spines developed, their papular areas are bifurcating, the accessory inferomarginal spines were probably relatively small and there are only 21½ adambulacrals matching the first ten inferomarginals on the only arm of which sufficient remains to allow a count. Two much larger specimens again from the Gulf of Guinea but off western Nigeria (*Pillsbury* st. 314, *c.* 5° N, 4° E, 2300 m), R ?130–150 mm, both have only a single disc spine and a few enlarged spinelets, the pore areas bifurcate, the accessory inferomarginal spines are less than half as long as the main spine and there are only *c.* 21 adambulacrals corresponding to the first ten inferomarginals but the subambulacral spines are predominantly two. These few specimens indicate that in the Gulf of Guinea at least, the development of disc spines and a second subambulacral spine is relatively retarded. Whether or not this is sufficiently consistent to justify retention of *B. chardyi* as a distinct taxon remains to be seen from further material. At present it seems best to treat it as a subspecies of *B. simplex.*

Similar doubts about the specific validity of *B. folini* must exist considering the inclusion in the type material of at least two specimens with conspicuous large odd superomarginal spines interradially, not the small multiple spines supposed by Perrier to be characteristic of the species. (Most of the remaining paratypes have lost these spines in preservation.) The larger of these two probably had R *c.* 50 mm and the single subambulacral spines would be expected in *B. simplex* at this size. It should also be noted that the holotype of *B. chardyi* has multiple small spines on one of its five odd superomarginal plates.

Since the recognition of multispinulose specimens as conspecific with *B. simplex,* only the numerous oral furrow and suboral spines in the holotype of *B. fischeri* at R only *c.* 40 mm serve to distinguish it. In spite of this and the presence of two subambulacral spines on most proximal plates, I think it not unlikely that further material from the type locality off NW Africa will show the holotype to be only an aberrant *B. simplex*.

RANGE. From the vicinity of Cape Cod (42–40° N, 63–66° W) south to the Gulf of Mexico, the Colombia and Guyana Basins and from south of Iceland (*Thor* st. 164) and the Rockall Trough (*c.* 57° N, 10° W) south to the Gulf of Guinea (*c.* 2½° S, 8° E); 1175–2585 metres.

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Observations of clonal cultures of Euglyphidae (Rhizopoda, Protozoa)

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Introduction

The identification of small siliceous testate amoebae is often difficult due to three main factors, observations are made at the limits of the optical microscope, scarcity of specimens and inadequate descriptions. The introduction of scanning-electron microscopy for detailed surface examination has reduced the first of these obstacles, as this facility permits more accurate descriptions to be made of the shells of these animals. However, matching these more detailed descriptions with existing reports is often complicated as slight differences of shell structure have frequently prompted authors to propose new specific names, or new 'varieties' or new 'forms'. The second factor can also be reduced by establishing clonal cultures in the laboratory; additionally such cultures enable one to study biology and variation in morphology. Previous reports (Hedley & Ogden, 1973, 1974; Hedley *et al.*, 1974) dealt with the biology of four species, namely *Euglypha acanthopora* (Ehrenberg, 1841), *E. rotunda* Wailes, 1911, *E. strigosa* (Ehrenberg, 1871) and *Trinema lineare* Penard, 1890.

The present account describes the shell morphology and biology of four further species, based on clonal cultures, together with the redescription of a previous clone under a new specific name.

Systematics

The genera *Euglypha* and *Assulina* belong to the family Euglyphidae—the classification adopted here is that proposed by Levine *et al.*, 1980 and Loeblich and Tappan, 1964:

Superclass	RHIZOPODA	Von Siebold, 1845
Class	FILOSEA	Leidy, 1879
Order	GROMIIDA	Claparede and Lachmann, 1859
Superfamily	EUGLYPHACEA	Loeblich and Tappan, 1961
Family	EUGLYPHIDAE	Wallich, 1864 shell hyaline, symmetrical, elongate, composed of rounded siliceous plates, aperture rounded or elongate; one nucleus.

Euglypha acanthophora—In identifying specimens from a clonal culture as *E. acanthophora* Hedley *et al.* (1974) accepted the reported variation attributed to this species, although with some reservation because the extent of the variations was not substantiated by our observations of other *Euglypha* species in culture. These differences mainly concerned the shape and position of the siliceous spines and the shape of the body plates, which are illustrated in Leidy's superb figures (Leidy, 1879) of *E. alveolata*—a species accepted by both Cash *et al.*, (1915) and Penard (in Cash *et al.)* as a synonym of *E. acanthophora*—showing that the siliceous spines project either distinctly from the sides of the body or discretely from the aboral extremity, and that there are distinct tooth-like projections on the posterior edge of the body plates. Penard (1902) proposed two varieties to accommodate specimens with

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varying spines, and these were accepted by Cash *et al.*, (1915) who also suggested that intermediate forms existed. The extent of these variations is given by Decloitre (1962) in a review of the genus *Euglypha*, which lists seven varieties of *E. acanthophora*.

The limitation of our research was such that it was expedient at that time (Hedley *et al.*, 1974) to consider our clonal culture to be representative of *E. acanthophora*. The problem of designated names now arises with the establishment of another distinct clonal culture within the heterogenous description of *E. acanthophora*. It appears that the most recent culture is more closely allied to the description of *E. acanthophora*, whilst the earlier culture (Hedley *et al.*, 1974) fits the description of *E. a.* var. *brevispina* given by Cash *et al.*, (1915). However, this latter description does not agree with the original (Penard, 1902) as discussed on p. 140, so to avoid confusion with these variety names it is proposed that a new specific name, *E. cashii*, be given to the earlier clonal culture.

Materials and methods

Information on the source of each species is given with the taxonomic description.

The animals were obtained from crude cultures made by isolating small portions of each sample placed in a small plastic container and covered with a shallow layer of the culture liquid. Agnotobiotic cultures were kept at room temperature (18–20°C), in similar containers, on a thin layer of agar agar (1 per cent in distilled water) with a sterilised wheat grain added prior to setting and covered by a shallow layer of culture medium. The culture medium was a 5 per cent solution of soil extract plus added nutrient salts (see Hedley & Ogden, 1973). Clonal cultures were established by isolating single active animals, and one clone has been used subsequently to produce the working cultures of each species. Subcultures made at 2–3 week intervals are adequate to maintain active animals.

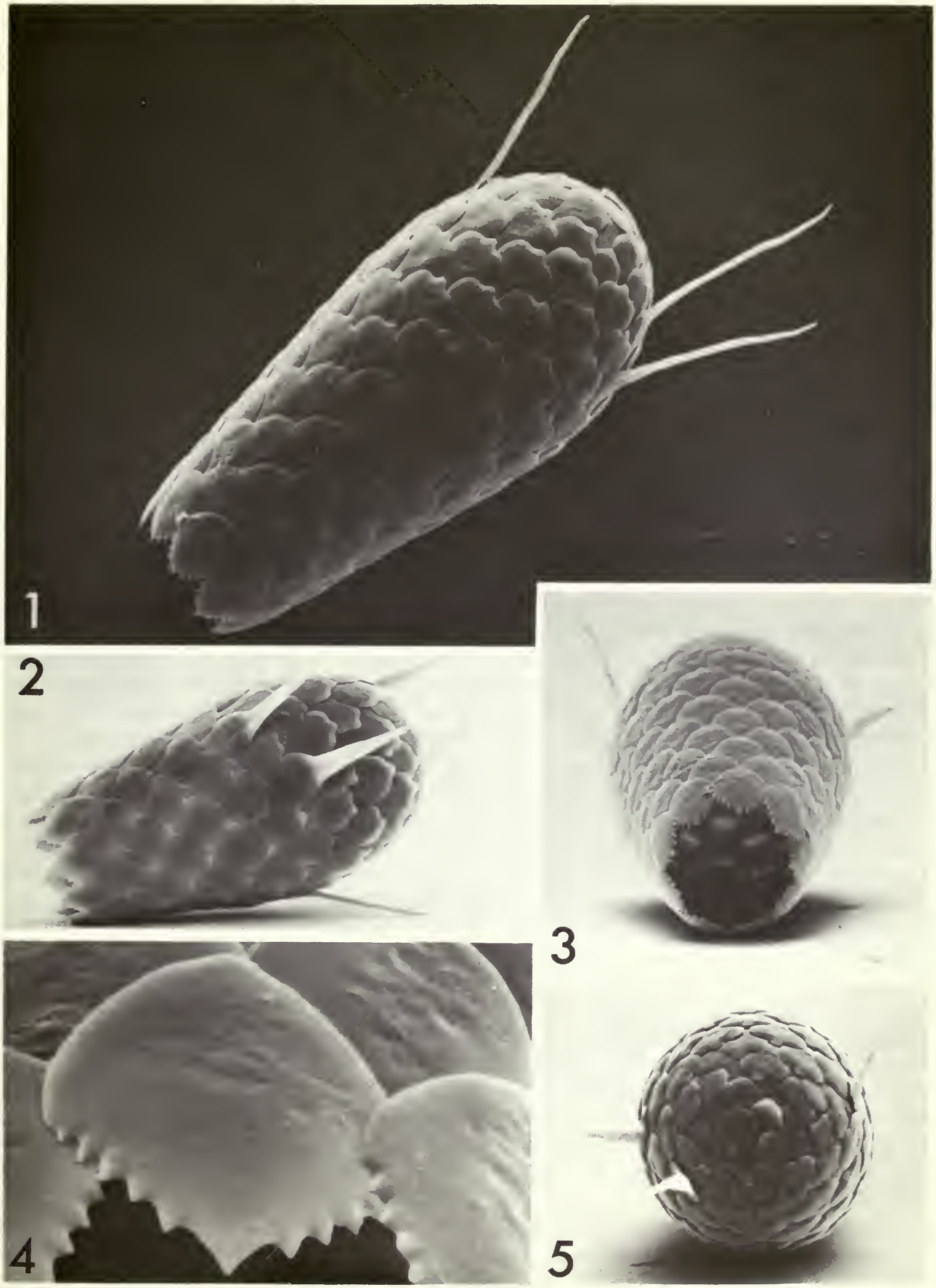
Live specimens were examined by optical microscopy using both phase-contrast and brightfield illumination. Specimens for scanning electron microscopy were cleaned by transferring them through several changes of distilled water. Then manipulated using a single-hair brush onto small drops of Araldite adhesive on a small cover slip, the cover slip having been previously cleaned and dried. The exception to this procedure were specimens of *E. dickensii* which proved to be fragile and collapsed using this technique. Alternatively they were fixed in 3 per cent glutaraldehyde in O·1M cacodylic acid buffer, rinsed in the buffer solution and several times in distilled water, then specimens in distilled water were micropipetted onto a clean cover slip and allowed to dry. Although some specimens still collapsed, the majority retained their natural shape. The prepared cover slips were fastened to aluminium stereoscan stubs with Araldite, prior to being coated evenly with a thin layer of conducting metal. The stubs were examined on a Cambridge Stereoscan 180 operating at 10kV and the results recorded on Ilford HP5 film.

Morphology

Euglypha acanthophora (Ehrenberg, 1841)

syn. *Euglypha alveolata* (Dujardin, 1841)—in Leidy, 1879, pl. 35, figs 3, 7, 15–18
Euglypha brachiata Penard, 1902 (Non Leidy, 1878)
Euglypha brachiata var. *flexulosa* Penard, 1902
Euglypha brachiata var. *brevispina* Penard, 1902 (Non Cash *et al.*, 1915)
Euglypha armata Wailes and Penard, 1911
Euglypha crenulata var. *minor* Wailes, 1912
Euglypha acanthophora var. *dorsalis* Schönborn, 1962

This species was isolated from a sample of *Sphagnum* moss collected at Holmsley, near Burley, New Forest, Hampshire, in March 1979.



Figs 1–5 *Euglypha acanthophora*: Figs 1 & 2, lateral views to illustrate the distribution of body and elongated plates × 1250 & × 970; Fig. 3, view of aperture with nine apertural plates × 1170; Fig. 4, single apertural plate, note the slight thickening on the dentate margin × 7500; Fig. 5, terminal or aboral view showing the distribution of oval body plates × 1200.

Table 1 Range of measurements (in μm).

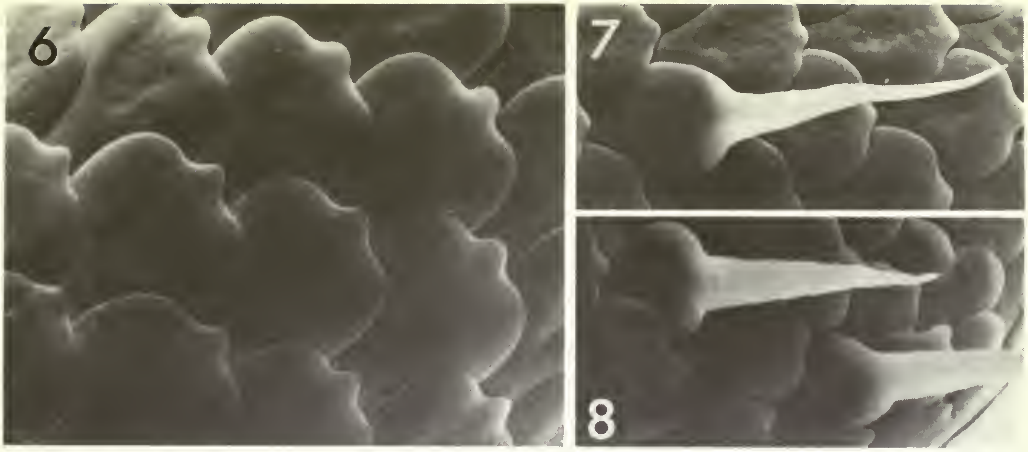
		length	breadth	depth	diameter of aperture
Euglypha acanthophora	(35)	54·4–68·6	26·4–33·8		12·8–16·5
Euglypha cashii	a.* (53)	65·1–84	33·6–42		16·8–25·2
	b. (10)	67–88·9	33·9–39·8		15·3–19·2
Euglypha compressa	(31)	60·8–74·7	36·2–46·4	19·7–25·6	12·1–17·7
Euglypha dickensii	(32)	35·3–53·5	20·7–34·4	14·1–18·9	9·1–14·7
Assulina muscorum	(33)	33·7–54	25·2–36·6	15·4–19·6	7·7–14·1

* measurements from Hedley *et al.*, 1974; bracketed figures indicate the number of specimens measured.
a. Clone from Hertfordshire, b. clone from Wales.

Description. The shell is elliptical or ovoid, circular in cross section, composed of about one hundred and thirty body plates and up to six elongated plates or spines (Table 1, Figs 1 & 2). The aperture is terminal, circular and surrounded by between eight and eleven, usually evenly spaced, denticulate apertural plates (Fig. 3). Each apertural plate is roughly oval, between 8·1–10·4 μm in length and 6·3–7·8 μm in width, often both the denticular and the opposite margin are pointed (Fig. 4). The dentate edge is barely thickened on the inner surface around the median tooth and the five smaller lateral teeth positioned on each side (Fig. 4). Denticular margins are also seen on the second circle of plates surrounding the aperture. The body plates are arranged in alternate, longitudinal rows, and range from 7·5–9·8 μm in length and 6·3–8·1 μm in width. Usually the posterior margin of these roughly oval plates has a median rounded projection, this appears to be more pronounced when the plate has an angular shape (Fig. 6). Body plates appear to vary in shape depending on their position, the pointed posterior margin of the plate becoming more pronounced in progression down the length of the body (Fig. 1), only to be rounded in some instances at the aboral extremity (Fig. 5). The elongated plates are dagger shaped, ranging in length from 18–30 μm, and usually project from the sides of the body at an acute angle (Figs 1 & 2). They may be positioned anywhere in the posterior half of the shell, but are only rarely seen projecting from the extremity. The elongated portion of these plates is thin, hence their brightness when bombarded by electrons in the scanning electron microscope (Figs 7 & 8), and vary markedly in breadth which in turn alters the degree of tapering. It would appear that narrow and long spines are more flexible (Fig. 7), whilst the broader and shorter spines are more robust (Fig. 8).

Discussion. Both Cash and Penard described *E. acanthophora* with long thin spines and *E. acanthophora* var. *brevispina* with short stout spines. There is good agreement between the diagrams of *E. acanthophora* given by Cash (1915: pl. 35, fig. 2), Leidy (1879 pl. 35 figs 3, 7, 15–18) and Penard (1902 p. 505 and in Wailes & Penard, 1911: pl. 3, fig. 16), but not between the diagrams for *E. a.* var. *brevispina,* those of Cash and Leidy (1915: pl. 33, figs 3, 5; 1879 pl. 35, figs 1, 2, 4) being quite different from the original Penard figures (1902 p. 505 figs 6–10). Whereas the spines shown by the former authors are pointed, Penard's are blunt and appear to have broken or ragged edges. As Penard's two varieties—*brevispina* and *flexulosa*—differ only in having as their names imply either truncate or flexous spines, features which are considered to be artifacts from observations on clonal cultures reported here, they are listed as synonyms of *E. acanthophora*.

Although the apertural plates in the above mentioned descriptions are similar, there are differences in the distribution and shape of the body plates. For example, Leidy (1879) noted that there were two rows of denticulate plates surrounding the aperture and that the body plates had small projections from their posterior margins. Both Cash and Penard agree with



Figs 6–8 *Euglypha acanthophora*: Fig. 6, area of shell surface showing typical body plates × 3300; Fig. 7, 'dagger-shaped' elongated plate, a narrow and flexible type × 2500; Fig. 8, a stout and robust type of elongated plate × 2700.

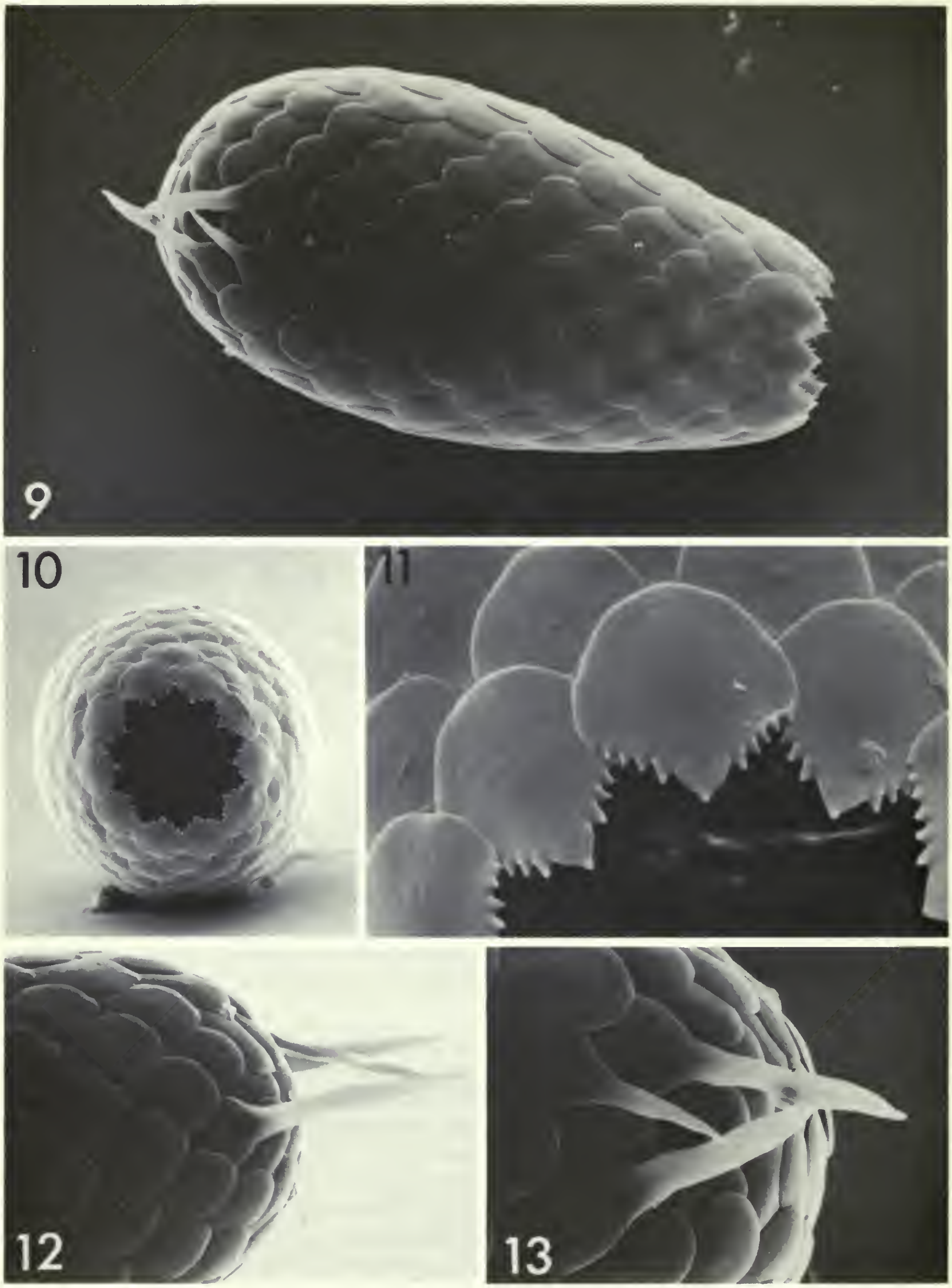
the two rows of denticulate plates, but neither commented on the body plates–except for a reference in the generic discussion (Cash *et al.,* 1915: p. 5) naming just three species with 'scutiform' plates: *E. scutigera* Penard, 1911; *E. aspera* Penard, 1899 and *E. crenulata* Wailes, 1911—nevertheless they synonymize Leidy's description with *E. acanthophora.* Wailes (1912) in describing a new variety, *E. crenulata var. minor,* noted that it was only distinguished from *E. armata* Wailes & Penard, 1911 (a synonym of *E. acanthophora* proposed by Wailes in Cash *et al.,* 1915) by the shape of the body plates.

Of the eleven varieties listed by Decloitre (1962, 1976), two have already been mentioned, *E. a.* var. *brevispina* and *E. a.* var. *flexulosa*; four appear to be similar to *E. acanthophora* as described here, these are *E. a.* var. *cylindracea* (Playfair, 1918), *E. a.* var. *dorsalis* Schönborn, 1962, *E. a.* var. *fantastica* Decloitre, 1965 and *E. a.* var. *longispina* Decloitre, 1969; two, *E. a.* var. *equeis* Decloitre, 1956 and *E. a.* var. *heterospina* Decloitre, 1949, have discrete arrangements of spines and may represent distinct species; and the remaining three are considered later on p. 143. The four similar varieties differ in size (*cylindracea*), slight deflection of the aperture (*dorsalis*), the shape of the spines (*fantastica*), and the number of spines (*longispina*). Specimens with misaligned apertures are not uncommon in clonal culture, and *E. a.* var. *dorsalis* is therefore considered to be a synonym of *E. acanthophora.* The differences of the three remaining varieties may also be artificial, but it is not possible to comment further on these.

Euglypha cashii nom. nov.

syn. *Euglypha acanthophora* var *brevispina*—in Cash *et al.,* 1915
Euglypha alveolata—in Leidy, 1879: pl. 35, figs 1, 2, 4
Euglypha alveolata var. *cirrata* Wailes, 1912
Euglypha acanthophora var. *deflanderi* Decloitre, 1956
Euglypha acanthophora var. *elegans* Stepanek, 1963
Euglypha acanthophora—in Hedley *et al.,* 1974
Euglypha acanthophora—in Ogden & Hedley, 1980

Two clones of this species have been isolated, the first from sewage sludge from the Maple Lodge Works of the Colne Valley Sewage Board, Hertfordshire, in December, 1972 and the second from a sample of *Sphagnum* moss from Myndd Hiraethog, Denbigh, Clwyd, North Wales, in August, 1980.



Figs 9–13 *Euglypha cashii*: Fig. 9, lateral view showing the distribution of body and elongated plates × 1250; Fig. 10, aperture with ten evenly distributed apertural plates × 1100; Fig. 11, detail of apertural plates × 4400; Fig. 12, elongated plates projecting from aboral extremity × 1800; Fig. 13, elongated plates following the curvature of the shell × 2400.

Description. The shell is elliptical or ovoid, circular in cross section, composed of about two hundred body plates and up to six elongated plates (Table 1, Fig. 9). The aperture is terminal, circular and surrounded by between ten and thirteen evenly spaced denticulate apertural plates (Fig. 10). Each apertural plate is roughly oval, varying from 8·1–12·5 µm in length and 7·2–11·5 µm in width. The dentate edge is slightly thickened and carries a median tooth with either four or five smaller lateral teeth on each side (Fig. 11). Specimens are sometimes seen with the average number of plates surrounding the aperture but with either one or two being dentate body plates, similar to those shown in Fig. 1a of Hedley *et al.* (1974), instead of dentate apertural plates. The body plates are arranged in alternate longitudinal rows and range from 10·9–12 µm in length and 7·9–9·1 µm in width. Each oval body plate has a median rounded projection on the posterior margin, these projections are not as pronounced as in *E. acanthophora* (compare Figs 1 & 9). The elongated plates project slightly from the aboral extremity, or closely follow the outline of the shell in the aboral region, they range from 19·6–29·2 µm in length and 6·1–7·6 µm in width (Figs 12 & 13).

Discussion. The description of this species is in good agreement with that given by Cash *et al.* (1915: pl. 33, figs 3 & 5) for *E. a.* var. *brevispina.* As there is some disparity between these two descriptions and the original description of the variety *brevispina* given by Penard (1902) (see also p. 140), in addition to the variety name *brevispina* being used with other species of *Euglypha,* it was considered that a new specific name would eliminate future confusion of these species. *E. cashii* is distinguished from *E. acanthophora* by size, shape of body and elongate plates, but mainly by the positioning of the elongated plates.

The three varieties of *E. acanthophora* listed by Decloitre (1962, 1976) which are similar to *E. cashii* are *E. a.* var. *cirrata*: *E. a.* var. *deflanderi* and *E. a.* var. *elegans,* they apparently differ only in the deflection of the posterior spines or elongated plates to the shell body. Such features have been seen in clonal culture as a normal variation, and these varieties are therefore considered to be synonyms of *E. cashii.* Another species, *E. tiscia* Gal, 1969, listed by Decloitre (1976), although similar to *E. cashii* is considered to represent a valid species because of its larger dimensions.

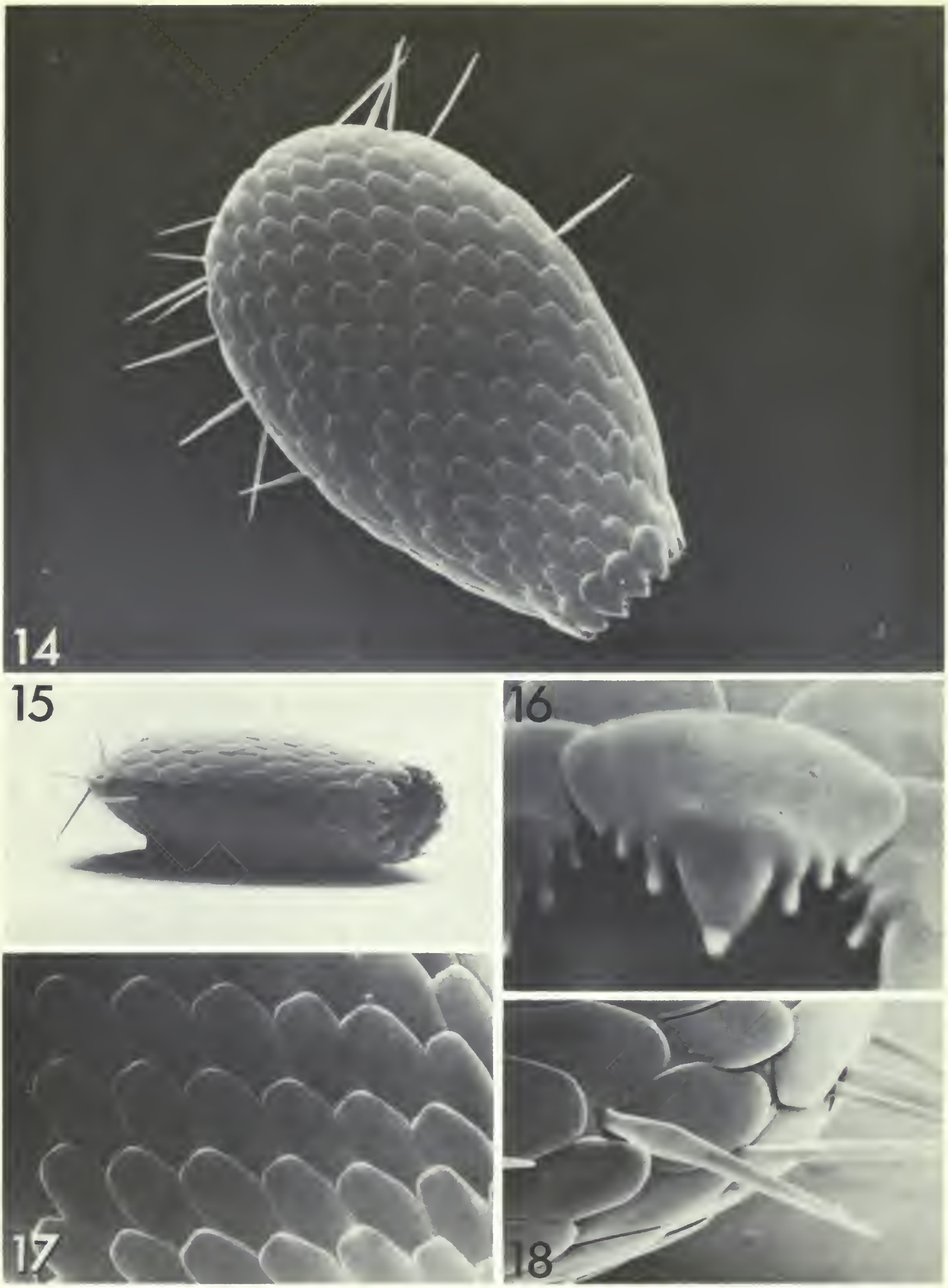
Etymology. This species is named after Mr James Cash, who contributed so much to the taxonomy of testate amoebae at the beginning of this century.

Euglypha compressa Carter, 1864

This species was isolated from a sample of *Sphagnum* moss, collected at Subberthwaite, Broughton in Furness, Cumbria, in July, 1978.

Description. The shell is ovoid, laterally compressed and composed of about two hundred body plates and thirty spines (Table 1, Fig. 14). The aperture is terminal, circular or elliptical and surrounded by between eleven and fifteen, evenly spaced, denticulate apertural plates (Fig. 15). Each apertural plate is oval, between 6·2–7·1 µm in length and 4·6–5·4 µm in width. The dentate edge is distally thickened around the large median tooth, but this thickening tapers evenly outwards to the three smaller teeth positioned on each side and equates with the normal shell thickness close to the last tooth (Fig. 16). The body plates are arranged in sequence and range in size from 7·4–8·2 µm in length and 3·4–4·4 µm in width. They are roughly oval and often characterised by their hexagonal appearance, this latter feature is variable but the squared nature of the narrow margins is usually distinctive (Fig. 17). The spines are positioned along the lateral margins from about the mid-body position to the aboral extremity (Fig. 15). They are sometimes in pairs and usually alternate when viewed laterally, one pointing upwards and the next downwards along the length of the body (Figs 14 & 15). Each spine has a narrow base from which it tapers to its widest point about a quarter of the total spine length, then it tapers gradually over the remaining threequarters to the terminal point (Fig. 18).

Discussion. The only recorded variety of this species is *E. compressa* f. *glabra* Cash *et al.,*



Figs 14–18 *Euglypha compressa*: Fig. 14, lateral view showing the distribution of body plates and spines × 1250; Fig. 15, latero-apertural view to illustrate the circular aperture and the positioning of the spines × 910; Fig. 16, detail of single apertural plate, note the thickening around the dentate margin × 9500; Fig. 17, arrangement of typical body plates × 2350; Fig. 18, illustration of spine projecting from organic cement matrix between two adjacent body plates × 4400.

1915, a form without spines. However, variation in the shape and size of the siliceous spines was also reported by Cash *et al.* for *E. compressa,* and such differences were considered to be a normal feature. This may not now prove to be the case, if, as the information derived from clonal cultures in the present work shows that differences in spine positioning is specific, then it would appear to follow that structural differences of spine construction may also be specific. The spines described here are similar to those reported by de Graaf (1956) and Brown (1910), but they are different from those described by Ogden & Hedley (1980). In the latter report the spines are stout at the base, concave, and taper evenly to a point (see Pl. 78D, Ogden & Hedley, 1980). Both types of spine are here considered to represent *E. compressa,* which is distinguished by the compressed shell and lateral position of the spines, but further work on clonal cultures may establish spine shape as a specific character.

Euglypha dickensii sp. nov.

This species was isolated from a sample of damp moss taken from underneath sweet chestnut trees at Cobham woods, Rochester, Kent in February, 1974.

Description. The shell is ovoid, laterally compressed and composed of about two hundred and eighty elongate body plates (Table 1, Figs 19 & 20). The aperture is terminal, oval or circular, and surrounded by between eleven and fifteen, evenly spaced, denticulate apertural plates (Fig. 21). In a few specimens additional apertural plates are seen in the second circle of plates around the aperture. Each apertural plate is roughly circular, from 5·4–6·4 µm in length and 3·8–4·4 µm in width. The dentate edge has a large, thick, distinctly curved, median process with a terminal pointed tooth, this is flanked on each side by a medium outward facing tooth and one or two smaller teeth (Figs 22 & 24). The denticular thickening equates with the normal shell thickness at the position of the small teeth. The body plates are elongate, ranging from 5·1–6·2 µm in length and 1·6–2·5 µm in width, and are arranged in alternate longitudinal rows. Around the mid-body region there are some randomly distributed pointed body plates (Fig. 23). These pointed plates vary from normal plates with a small sharp spike, about 6·9 µm long, to tapered spines about twice the length, 9·1 µm, of a normal body plate. Although there is variation in the dimensions of these pointed body plates, their presence in a mid-body position is a reasonably stable feature.

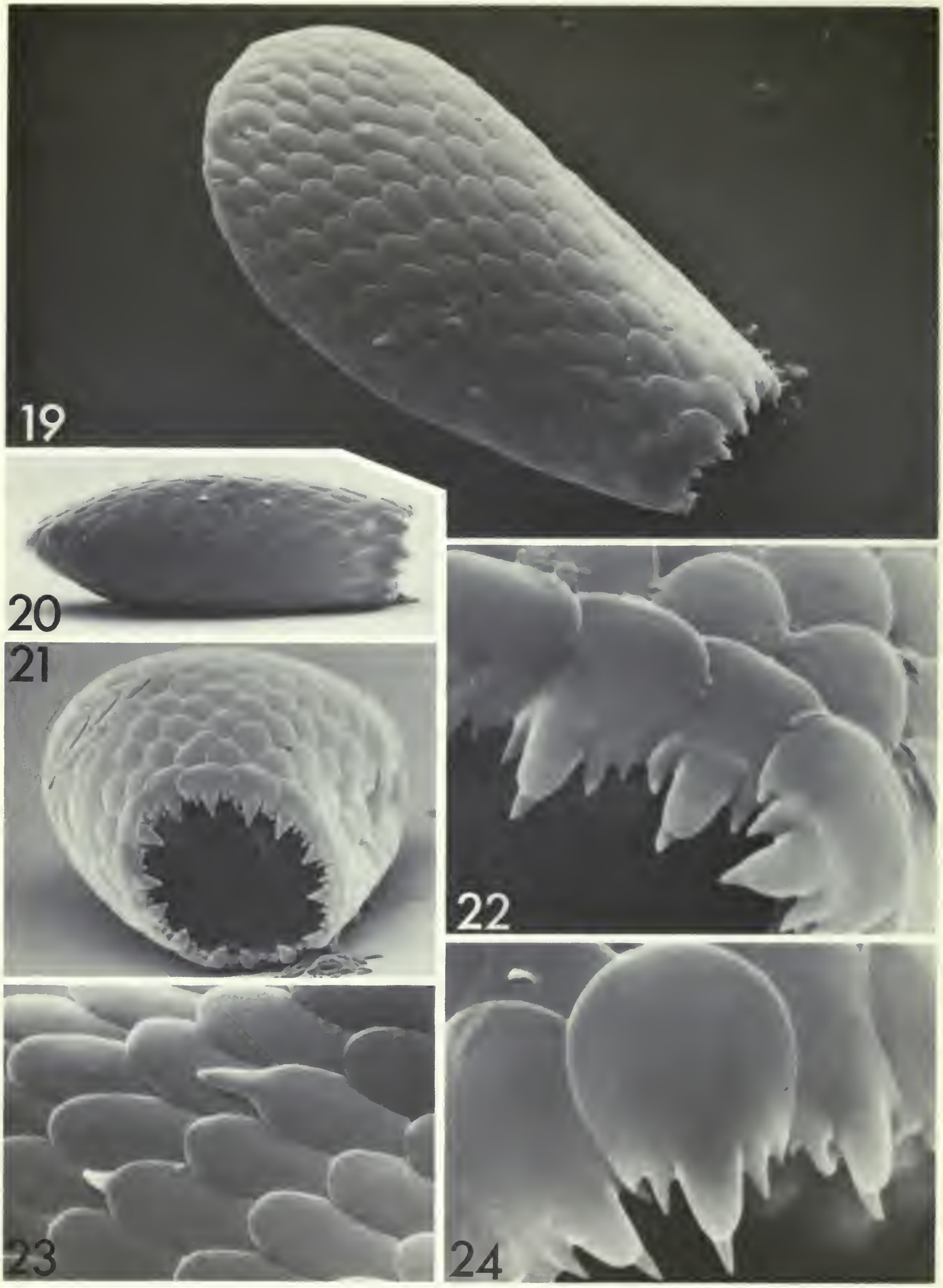
Discussion. The species described here is similar to three species previously reported from soil samples, namely *E. capsiosa* Couteaux, 1978, *E. cuspidata* Bonnet & Thomas, 1960 and *E. simplex* Decloitre, 1965. It has similar dimensions to *E. simplex* but differs in the shape of the apertural plates, which in the latter species have a distinct diamond-shape (see Couteaux *et al.,* 1979). Both *E. capsiosa* and *E. cuspidata* are smaller species with fewer body and apertural plates, and again differ in the shape of the apertural plates. *E. dickensii* is distinct in size, dentation of the apertural plates and the presence of pointed body plates in the mid-body region.

Etymology. As this species was found in the countryside frequented by Charles Dickens, the nineteenth century author, and subsequently featured in many of his novels, it is named in his honour.

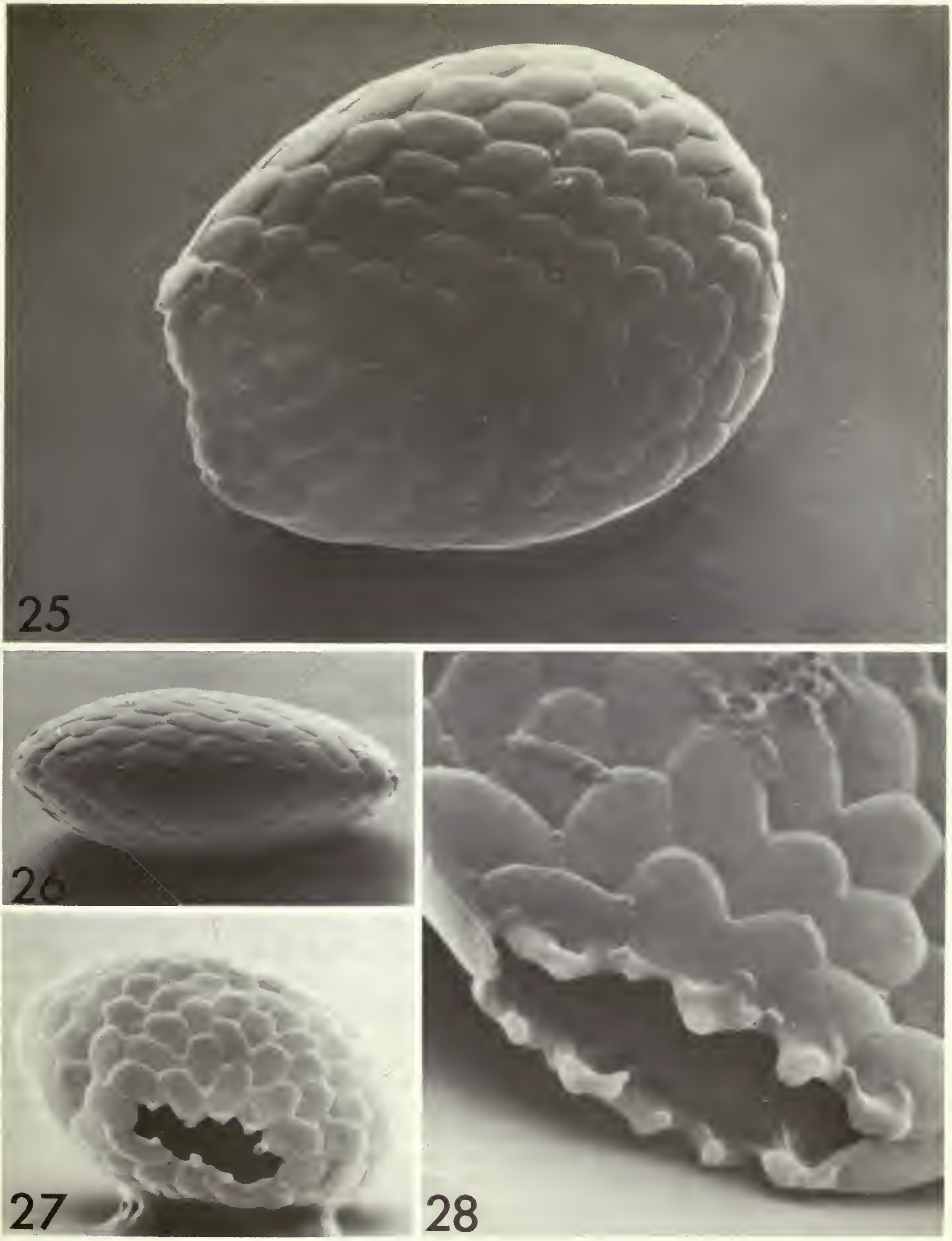
Assulina muscorum Greef, 1888

This species was isolated from a sample of dry moss on soil, collected at Rolestone Farm, Banwell, Somerset in February, 1974.

Description. The shell is ovoid, laterally compressed and composed of about two hundred shell plates (Figs 25 & 26). The aperture is terminal and surrounded by between ten and fourteen shell plates arranged in a rather irregular manner, most with their minor axis bordering the opening but often a few have their major axis (Figs 27 & 28). The opening is edged with a thin band of organic cement, this band is frequently thickened on the tips of some plates to form tooth-like projections (Fig. 28). The shell plates are oval, ranging from 5·8–6·8 µm in length and 2·5–3·1 µm in width. They are usually arranged in alternate,



Figs 19–24 *Euglypha dickensii*: Fig. 19, lateral view showing the distribution of body plates × 1970; Fig. 20, view to illustrate the lateral compression × 1300; Fig 21, aperture with fourteen apertural plates × 2400; Fig. 22, view showing the overlapping of the apertural plates and the thickness of the median tooth × 7800; Fig. 23, portion of shell surface with two pointed body plates × 4600; Fig. 24, circular apertural plate with typical dentate margin × 11000.



Figs 25–28 *Assulina muscorum*: Fig. 25, lateral view to illustrate the distribution of shell plates × 2150; Fig. 26, view to show lateral compression and arrangement of plates × 1400; Fig. 27, apertural view × 2100, Fig. 28, detail of 'tooth-like' projections of organic cement around the aperture × 4900.

longitudinal rows, with their major axis parallel to the major axis of the body. However, in some instances the axes of the plates are not parallel with the body and in these cases the general pattern is altered. The aboral extremity is also subject to irregular arrangements of shell plates.

Discussion. The shell of *A. muscorum* is reported as being usually brown but occasionally colourless in the wild, whereas in culture it is mainly colourless. Nevertheless, live animals have a distinct band, probably the 'pigment zone', at the mid-body region which is often so large that it may tend to give colour to the shell. Variation in structure of the shell appears to be limited to the formation of an extra large individual, usually confined to less than three per cent of the population. Such specimens have more than the normal compliment of shell plates but the arrangement is the same. Similar large specimens have been reported (Hedley & Ogden, 1973) in clonal cultures of *Euglypha rotunda.*

Reproduction

The formation of a daughter-cell by simple division has been observed for all the described species and follows the same pattern in each, the only variation being the additional arrangement of elongated plates or spines in *E. acanthophora, E. cashii* and *E. compressa.* The sequence of events in *E. compressa* are described.

Euglypha compressa

The onset of division begins with the protrusion of a short thick cytoplasmic extension from the parent aperture. The apertural plates are the first to be passed from the storage area adjacent to the nucleus, via the peripheral cytoplasm to become arranged in a circle around this cytoplasmic extension. The remainder of the plates follow the same route and are arranged in sequence, in distinct rows radiating from the apertural plates (Fig. 29a). Each plate is added on the inside of the previous plate so that there is a considerable overlap. This excessive overlapping of the plates in the region of attachment is very noticeable in the early stages of shell construction. All the body plates are therefore in position, but not correctly spaced, well in advance of the shell attaining its full size. When the daughter shell has attained a size about two-thirds that of the parent, vacuolar activity is seen in the anterior third of the parental cytoplasm. This activity proceeds into the daughter cytoplasm as it increases in volume, at the same time the zone of pigment granules begin to extend towards the aperture of the parent. The spines are the last elements to be passed from the parent to the daughter (Figs 29b & c), where they are arranged centrally in the cytoplasm parallel to the shell walls. The pair of mid-body spines are the first to be pushed by cytoplasmic

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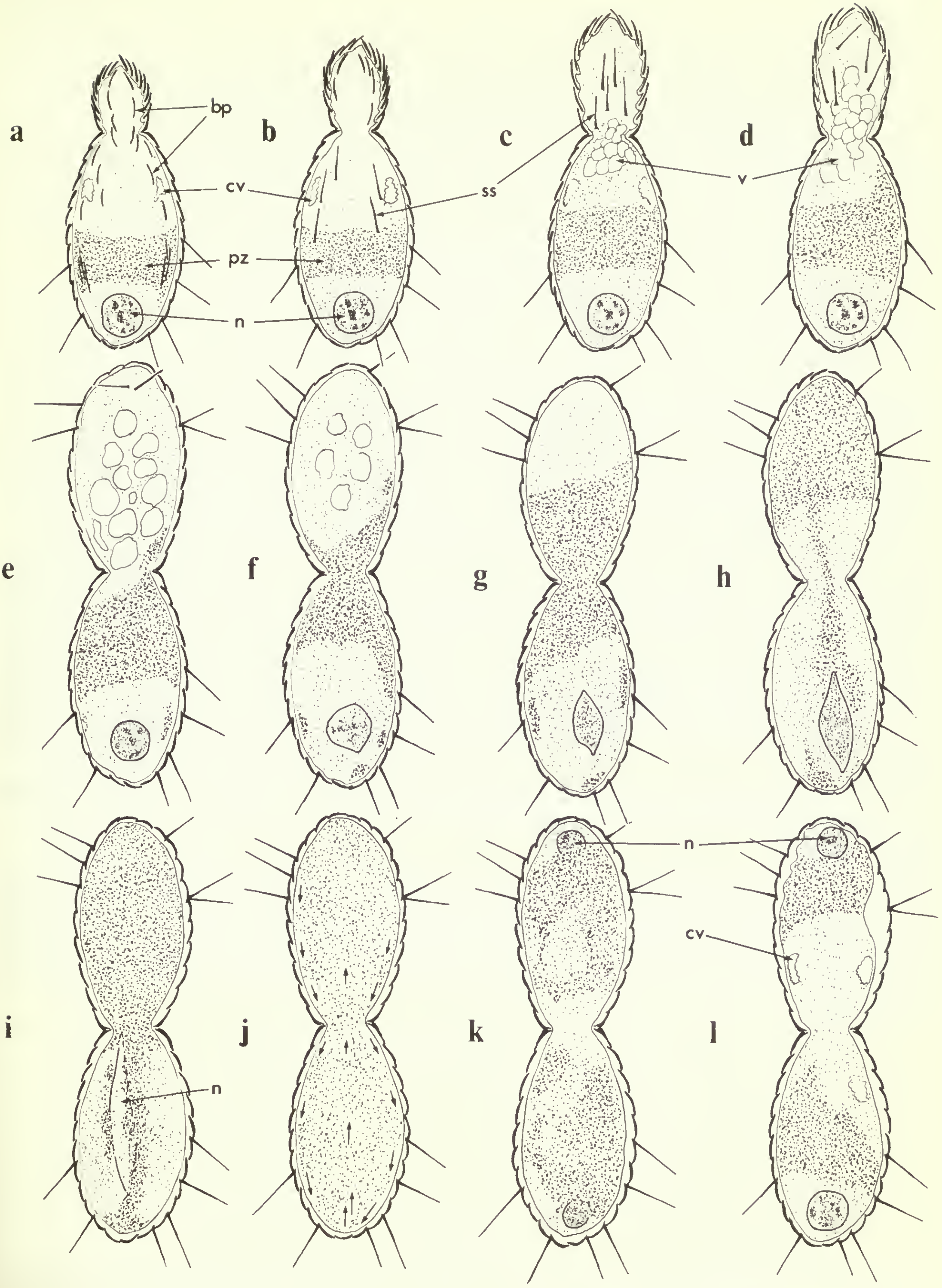
Fig. 29 Diagram illustrating division in *Euglypha compressa*: formation of daughter shell **(a–e)** followed by nuclear division **(f–l)**.
a. body plates (bp) pass via the peripheral cytoplasm to extremity of cytoplasmic extension of parent, 10–15 minutes; **b.** as last plates pass into forming daughter shell, siliceous spines (ss) begin moving from parent, 20 minutes; **c.** spines move into daughter shell, cytoplasmic vacuoles (v) appear close to parent aperture and granules of pigment zone (pz) begin to move, 25 minutes; **d.** spines arranged for positioning in daughter, and granules in parent move towards aperture, 27 minutes; **e.** daughter shell full size with some spines in position and cytoplasm filled with cytoplasmic vacuoles, granules begin to extend from parent into daughter, 30 minutes; **f.** daughter shell complete, granules in position between the opposed apertures and nucleus (n) in parent has small polar extensions, 40 minutes; **g.** elongation of parent nucleus, 55 minutes; **h.** granules mainly in daughter and nucleus now 'diamond-shape', 60 minutes; **i.** elongated nucleus becoming indistinct behind moving granules, 70 minutes; **j.** arrows depict pathways of rapidly moving granules, 75 minutes; **k.** movement of granules has slowed down and zones beginning to reform, faint nucleii appear, 90 minutes; **l.** contractile vacuoles (cv) and nucleii apparent, pigment zones almost reformed, 100 minutes. The times given are based on an estimated starting point.


a
bp
b
c
d
cv
ss
v
pz
n
e
f
g
h
n
i
j
k
l
cv
n

movement out between adjacent, lateral body plates, they appear to be positioned on each side simultaneously. This pair are followed in succession by other pairs of spines in a progressive sequence towards the aboral region. The last spines to be positioned are those that project from the terminal region. These spines are manoeuvred in the cytoplasm (Fig. 29e) until they are parallel to the aboral shell surface, they are then pushed through and cytoplasmic movement continues until the spines are at right angles to the shell surface. Throughout the time taken to position the spines those that project from the shell are in continuous movement, backwards and forwards like oarsmen in a rowing-boat except that their movements are not synchronized, and there are smaller movements still visible amongst the body plates. Vacuolar activity seems to be concentrated mainly in the daughter with the pigment granules being pushed from the parent into the peripheral cytoplasm of the daughter. A halo effect is most noticeable around the parent nucleus at this time.

A few seconds after the last aboral spines are in position, movement of all the shell elements slows down, until the spines are projecting slightly posteriorly when viewed from above. All movement has stopped after a further two minutes from the final positioning of the last aboral spines, and the daughter shell is complete. At about the same time the parent nucleus begins to elongate, initially there are two small polar extensions (Fig. 29f), but this changes into a 'diamond-shape' as most of the granules are passed into the daughter cytoplasm (Fig. 29g). Slightly later, movement of the granules in the daughter cytoplasm seem to suggest that when they reach the aboral extremity they are reflected back via the peripheral cytoplasm to the parent, meanwhile the nucleus has become more elongate (Fig. 29h). Rapid movement of the granules now obscures the changing nucleus (Fig. 29i), and a regular pathway of constantly moving granules is formed between the parent and daughter cytoplasm (Fig. 29j). When the rapid movement ceases, after about five minutes it is replaced by a slow regular movement with no apparent directional flow, cytoplasm of both cells looking homogenous. After a further five minutes the apertural region of both are relatively free of granules, contractile vacuoles are apparent in the anterior region of each and there is some movement of granules (Fig. 29k). A little while later nuclei are apparent in the posterior region of both cells as the pigment granules are concentrated into the mid-body region (Fig. 29l). Just prior to separation the cytoplasm in each shell is withdrawn slightly so that the cytoplasmic connection is severed, the animals move apart independently shortly after this action.

The approximate time taken to produce the daughter shell is forty-five minutes, whilst the total time for division is one hundred minutes.

Doubling time

Estimations on the length of time required to double the population (doubling time) were made on cultures established and maintained under similar conditions. Growth curves calculated from records of daily counts of individuals were made on three replicate cultures of four species, but only one culture was available for *E. acanthophora*. The results are given in Table 2.

Table 2 Estimates of doubling time (in days).

Euglypha acanthophora	2·7
Euglypha cashii	2·3–2·8
Euglypha compressa	4·0–4·4
Euglypha dickensii	2·6–3·1
Assulina muscorum	2·3–2·9

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The Nuttall and British Museum (Natural History) tick collections: lectotype designations for ticks (Acarina: Ixodoidea) described by Nuttall, Warburton, Cooper and Robinson

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Introduction

A monographic revision of the Ixodoidea was begun by Nuttall *et al.* (1908) with subsequent volumes published by Nuttall & Warburton (1911, 1915) and Robinson (1926). A further volume was produced by Arthur (1960). These works were based largely on material gathered by Nuttall and his associates and the Entomological Research Committee for Tropical Africa, forerunner of the present day Commonwealth Institute of Entomology. During his lifetime, Professor Nuttall presented a considerable number of specimens to his correspondents. In 1939, the remainder of the Nuttall Collection was donated by the Molteno Institute to the British Museum (Natural History) and at that time it was the largest tick collection in the world. Currently, the Nuttall collection is kept separately from the main tick collection of the British Museum (Natural History), and types of Ixodoidea designated by Nuttall *et al.* may be found in both collections.

Prior to the formulation of the *International Code of Zoological Nomenclature*, type specimens were frequently labelled only as 'TYPE' or 'COTYPE' with the result that many of the taxa described by Nuttall *et al.* were in need of lectotype designations. Consequently these studies were undertaken and form the basis of the present report. At the same time an attempt was made to trace the type material of all taxa described by Nuttall and his associates; appendices are therefore provided listing holotypes, previously selected lectotypes and other types together with their location, where known.

The following list of lectotypes is in alphabetical order by specific name within the genera *Argas* and *Ornithodoros* in the family Argasidae and within the genera *Amblyomma, Aponomma, Dermacentor, Haemaphysalis, Ixodes, Rhipicentor,* and *Rhipicephalus* in the family Ixodidae. First the species binomen, or in a few cases the trinomen as originally described, is given followed by author(s), date, page, and figure(s). Any currently recognized synonyms and the Nuttall tick catalogue number precede a statement detailing all pertinent information relating to the original collection. Next, the current status of the type material is given, including selection of a lectotype and paralectotypes and an updating of the host and locality data. This is followed by subsequent published information relating to the species in question. Finally, there is a brief statement which summarizes hosts and distribution of each tick species.

During the course of the studies reported below, each lectotype and each paralectotypic series was isolated within the vial or jar containing specimens of the taxon; the nomenclative status of this material was clearly indicated on an additional included label.

Bull. Br. Mus. nat. Hist. (Zool.) **41**(4): 153–178·

Issued 26 November 1981

ARGASIDAE

Argas reflexus indicus Warburton, 1910 : 396.

NUTTALL 1649. 'The Indian Museum collection contained three specimens of this form. One was found in a book in the Entomological room, and another on a wall of the Museum building. The third specimen was found in a box sent from the Museum to Kurseong, E. Himalayas. The birds building in the roof of the Museum were identified as *Passer domesticus* and *Cypselus affinis*. The type species has not been recorded from India.'

TYPES. Lectotype ♀ *Argas reflexus indicus* (N1649) found in a book, Entomological room, Indian Museum, Calcutta (22°32′N, 88°22′E), India, 15.III.1910, C. A. Paiva. [Date and collector information taken from vial label].

REMARKS. A second collection (N1243) consisting of 1 ♂, 1 ♀, 1 N *A. reflexus indicus,* found in basin of water, Entomological room, Indian Museum, Calcutta, 13.IV.1910, F. H. Gravely, has a blue label with the word TYPE. We have not accorded these specimens paralectotype status because the specimen numbers and locality data do not conform to Warburton's published record.

Argas reflexus is not known to occur east of 15°00′ longitude and without additional collections, the exact taxonomic status of *A. r. indicus* remains moot.

HOSTS & DISTRIBUTION. *Argas reflexus indicus* is an avian parasite known only from India.

Ornithodoros gurneyi Warburton, 1926 : 55, fig. 1

NUTTALL 3562. 'Described from two specimens taken in an old shed at Tibboburra, N.S.W., 24.XI.1922, by Mr W. B. Gurney and sent with other ticks by the Government Entomologist of N.S.W. in 1924 to the Imperial Bureau of Entomology, where it was numbered 1378.'

TYPES. Lectotype ♂ *Ornithodoros gurneyi* (N3562) taken in an old shed, Pindera Selection, Tibboburra, New South Wales, Australia; 1 N paralectotype *Ornithodoros gurneyi,* date as above, deposited in the BM(NH) 97 collection (1925.5.9.4).

HOSTS & DISTRIBUTION. *Ornithodoros gurneyi* is primarily a parasite of large macropodids (kangaroos and wallaroos) but will also attack man and dogs in most areas of Australia.

Ornithodoros piriformis Warburton, 1981 : 285, fig. 2

NUTTALL 3335. 'Described from 15 specimens taken at Mahabaleshwar, Satara District, at a height of 4200 ft, (?host) by F. H. G., 13-16.IV.12. Indian Mus. SPA./10.'

TYPES. Lectotype ♀ and 2 ♀, 1 ♂ paralectotypes *Ornithodoros piriformis* (N3335) host unknown, Robber's Cave, Mahabaleshwar (17°55′N, 73°40′E), Maharashtra, India, at a height of 1280 m, 13–16.IV.1912, F. H. G.

REMARKS. The locality Robber's Cave is taken from Nuttall's catalogue and on the vial label with the ticks. Two slides, one with hypostome palp and leg I, the other with hypostome, are both missing.

HOSTS & DISTRIBUTION. *Ornithodoros piriformis* has been collected from *Miniopterus schreibersii* from the type locality. Robber's Cave contains several other bat species including *Rousettus leschenaulti* and probably *Rhinolophus affinis.* This tick is known only from India.

IXODIDAE

Amblyomma atrogenatum Nuttall & Warburton, 1908 : 409, figs 30–32

Junior subjective synonym of *Amblyomma clypeolatum* Neumann, 1899.

NUTTALL 43. 'Description based on 6 ♂ from *Testudo elegans,* received from India at the Zoological Gardens, London, 15.VIII. removed 2.X.1905. (Preserved in spirit.)'

TYPES. Lectotype ♂ and 4 ♂ paralectotypes *Amblyomma atrogenatum* (N43) ex *Testudo elegans* received from India at Zoological Gardens, London, 15.VIII.1905. Ticks removed 2.X.1905.

REMARKS. The 4 ♂ paralectotype total includes 1 ♂ pinned specimen. An empty token tube in the Nuttall collection indicates a slide mount of 1 ♂ which is now missing.

HOSTS & DISTRIBUTION. *Amblyomma clypeolatum* is a tortoise parasite in India and Sri Lanka.

Amblyomma caelaturum Cooper & Robinson, 1908 : 460, figs 6–9

Junior subjective synonym of *Amblyomma geoemydae* (Cantor, 1847).

NUTTALL 2938. Original description 'based on two ♂'s and one gorged ♀. Collected by Mr F. F. Laidlaw, Skeat Expedition, 1899, Kwala Aring, Java. Host, a tortoise (*Geoemyda spinosa*). Preserved in alcohol.'

TYPES. Lectotype ♂ and 1 ♂, 1 ♀ paralectotypes *Amblyomma caelaturum* (N2938), ex *Heosemys spinosa,* Kwala Aring, Malaysia (locality not verified) collected by Dr N. Annandale, 1899. Gift of Mr F. F. Laidlaw. Correction of locality and collector: Robinson (1926 : 230).

REMARKS. The name *A. caelaturum* was published in July, 1908. The name *A. maylanum* Neumann was published in March of the same year. Anastos (1950 : 107) sank the former as a junior synonym of *A. malayanum* on the grounds of priority. After examination of all relevant types Kohls (1957 : 87) concluded that both *A. caelaturum* and *A. malayanum* were junior synonyms of *A. geoemydae* (Cantor, 1847).

HOSTS & DISTRIBUTION. *Amblyomma geoemydae* parasitizes reptiles, especially tortoises and monitor lizards in Indonesia, Malaysia, Thailand, Ryukyu Islands, Japan, Taiwan, and the Philippines.

Amblyomma cooperi Nuttall & Warburton, 1908 : 410, figs 33–36

Junior synonyms: *Amblyomma lutzi* Aragão, 1908 : 112; *Amblyomma ypsilophorum* Schulze, 1941 : 93.

NUTTALL 70. Original description, 'based on 1 ♂ and 5 ♀ collected from "Carpinchio" (*Hydrochoerus capybara*) at Puerto Cooper, Alto, Paraguay, S. America, by W. F. Cooper in 1904. (Dry specimens.)'

TYPES. Lectotype ♂ and 1 ♂, 6 ♂ paralectotypes *Amblyomma cooperi,* (N70), ex *Hydrochoerus hydrochaeris* Puerto Cooper (23°03′S, 57°43′W), Alto, Paraguay, 1904, W. F. Cooper. [Included in the above total is one slide-mounted ♀].

REMARKS. Robinson (1926 : 75) indicated that more than 1 ♂ was present in the original collection but gave no total.

HOSTS & DISTRIBUTION. *Amblyomma cooperi* is a parasite of capybaras and tapirs in Paraguay, Bolivia, Brazil, Uruguay, and Argentina.

Amblyomma darlingi Nuttall, 1912 : 50, figs 1–4

Junior synonym of *Amblyomma oblongoguttatum* Koch, 1844.

NUTTALL 1285–1287. 'Described from 5 ♂, 9 ♀, 40 N, and 23 larvae found on a deer (*Odocoleus* sp.), Corozal, Panama Canal Zone, 14.VIII.1910, by A. H. Jennings, of Ancon, and 2 N, found on the nape and head of a turkey buzzard (*Catharista atratus*), Empire, Canal

Zone, IV.1911, by S. T. Darling, M. D., Chief of Laboratory, Isthmian Canal Commission, Ancon, Canal Zone. Named in honour of Dr Darling in view of his distinguished service to parasitology. The types, for which I am indebted to Dr Darling, are in Cambridge (N.1285–1287).'

Types. Lectotype ♂ and 2 ♂, 7 ♀ paralectotypes *Amblyomma darlingi* (N1285) ex *Odocoileus virginianus,* Corozal (08°59′N, 79°35′W), Panama, 14.VIII.1910, A. H. Jennings [above paralectotype total includes 1 ♂, 1 ♀ which were pinned and are now in the BM(NH) collection] 33N, 20L paralectotypes *Amblyomma darlingi* (N1286) same collection data as N1285; 2N paralectotypes *Amblyomma darlingi* (N1287) ex *Coragyps atratus,* perhaps from Empire Known Distance Range (09°04′N, 79°40′W), Panama, IV.1911, Dr S. T. Darling.

Hosts & distribution. *Amblyomma oblongoguttatum* occurs on a wide variety of mammalian hosts including deer, peccary, horse, cattle, dog, goat, armadillo, raccoon, etc., and ranges from the State of Sinaloa, Mexico, southward through Central America to Venezuela and Brazil.

Amblyomma fiebrigi Robinson, 1912 : 482, figs 3, 4

Junior subjective synonym of *Amblyomma pacae* Aragão, 1911.

Nuttall 2939. 'Described from 1 ♂ and 1 ♀, collected at San Bernardino, Paraguay, S. America, by Dr Karl Fiebrig. Host not specified.'

Types. Lectotype ♂ and 1 ♀ paralectotype *Amblyomma fiebrigi* (N2939), host unknown, San Bernardino (25°16′S, 57°19′W), Paraguay, Dr Karl Fiebrig.

Remarks. There is no date given for this collection in the original description but both Nuttall's tick catalogue and the vial label with the ticks bear the date 1911.

Hosts & distribution. *Amblyomma pacae* is most often collected, although not in large numbers, from *Agouti paca* but it has also been recorded from the genera *Dasyprocta* and *Tamandua.* This tick has been collected in British Honduras, Panama, Colombia, Venezuela, Brazil and Paraguay.

Amblyomma laticaudae Warburton, 1933 : 561, figs 5, 6

BM(NH) 1933.3.15.24–26. 'Described from 1 ♂, 1 ♀ (gorged) and 1 nymph taken from a sea-snake, *Laticauda colubrina.* The ticks were adhering to the skin, shed in captivity, at the Raffles Museum, Singapore, and were sent to Cambridge by the Assistant Curator, Mr Norman Smedley, who adds the following note: "The large ♀ and others were of the same grey as the snake and usually attached to the grey parts of the body, although I observed one on a black stripe. *Laticauda colubrina* belongs to that group of the sea-snakes possessing broad ventrals, and spends quite a considerable part of its time out of water, but even so the survival of the ticks while the snake is submerged seems remarkable." Types in the British Museum (Nat. Hist.).'

Types. Lectotype ♂ and 1 ♀, 1 N paralectotypes *Amblyomma laticaudae* BM(NH) 1933.3.15.24–26 ex *Laticauda colubrina*, Raffles Museum, Singapore (01°17′N, 103°51′E), Republic of Singapore, VI.1930, sent by Mr Norman Smedley.

Remarks. Collection date of VI.1930 taken from vial label.

Hosts & distribution. *Amblyomma laticaudae* has been collected only from *Laticauda colubrina,* a venomous sea snake which is widely distributed throughout the tropical Indo-Pacific Islands, southern Japan to the Bay of Bengal.

Amblyomma robinsoni Warburton, 1927 : 408, pl. xxvii, figs 1, 2

Nuttall 3617. 'Described from 8 ♂ and 3 ♀ taken from *Varanus komodoensis* and contained in a tube labelled "Komodo VII, 1923, Museum Buitenzorg," Java.'

TYPES. Lectotype ♂ and 2 ♂, 1 ♀ paralectotypes *Amblyomma robinsoni* (N3617), ex *Varanus komodoensis*, Komodo Island (08°35′S, 119°28′E), Lesser Sunda Islands, Indonesia, VII.1923, ex Museum, Buitenzorg, Java.

HOSTS & DISTRIBUTION. *Amblyomma robinsoni* is apparently restricted to the giant monitor, *Varanus komodoensis,* on Komodo Island.

Amblyomma uncatum Nuttall & Warburton, 1908 : 412, figs 37–40

Junior subjective synonym of *Amblyomma nodosum* Neumann, 1899.

NUTTALL 36. 'Description based on 5 ♂ from *Tamandua tetradactyla,* S. America (Zool. Society's Gardens, London, 1905. Dry specimens).'

TYPES. Lectotype ♂ and 6 ♂ paralectoypes *Amblyomma uncatum* (N36) [Lectotype and one paralectotype in alcohol, 2 paralectotypes pinned, 3 paralectotypes mounted on slides] ex *Tamandua tetradactyla,* South America, 1905.

REMARKS. The host (an anteater), from which the type series was collected, arrived at the Zoological Society's Gardens, London, 10.XII.1905 and died 22.XII.1905 (Robinson 1926 : 199). The date on the vial label is 22.XII.1905. There are also present two additional slides, one with the capitulum and leg IV of a ♂, and the second with chelicerae and hypostome of a ♂. Evidently, Nuttall & Warburton based their description on 5 of the 7 specimens comprising the collection.

HOSTS & DISTRIBUTION. *A. nodosum* adults are specific parasites of anteaters and the species has been reported from Costa Rica, Panama, Guatemala, Colombia, Bolivia, Nicaragua, Brazil and Trinidad.

Amblyomma v-notatum Nuttall, 1910 : 412, fig. 5

Junior subjective synonym of *Amblyomma geayi* Neumann, 1899.

NUTTALL 1149. 'Described from (N1149) 4 ♀'s found on a sloth (*Bradypus tridactylus*), at Manaos, Brazil, by Mr T. P. Beddoes, 1903.'

TYPES. Lectotype ♀ and 2 ♀ paralectotypes *Amblyomma v-notatum* (N1149) ex *Bradypus tridactylus* Manaus (03°08′S, 60°01′W), Brazil, 1903, T. P. Beddoes.

HOSTS & DISTRIBUTION. *Amblyomma geayi* is parasitic on both *B. tridactylus*, the three-toed sloth and *Choloepus* spp. two-toed sloths in Panama, Colombia, Guyana, Surinam, Brazil and Peru.

Amblyomma variegatum nocens Robinson, 1912 : 480, fig. 2

Junior subjective synonym of *Amblyomma pomposum* Dönitz, 1909.

NUTTALL 2941. 'Rhodesia, South Africa. Host not specified. Described from 2 ♂'s collected by Mr E. M. Jarvis, F.R.C.V.S., of the Dept. of Agriculture, Southern Rhodesia.'

TYPES. Lectotype ♂ *Amblyomma variegatum nocens* (N2941), Zimbabwe, Mr E. M. Jarvis.

REMARKS: There is no date given for this collection in the original description but both Nuttall's tick catalogue and the vial label with the tick bear the date 1911. Robinson (1926 : 100) stated that this collection was '?off cattle'. The second ♂ specimen of the type series could not be located.

HOSTS & DISTRIBUTION *Amblyomma pomposum* is most often collected from domestic cattle but is found on many other Artiodactyla. It is distributed in highland areas from Uganda and Zaire southward to Zambia.

Amblyomma versicolor Nuttall & Warburton, 1908 : 407, figs 27–29

Junior synonym of *Amblyomma cajennense* (Fabricius, 1787).

NUTTALL 212. 'Description based on 1 ♂ and 1 ♀ from a horse, Tolosa, Oaxaca, Mexico, collected by Mr A. Laughton, 1907. (Preserved in 70% spirit.)'

TYPES. Lectotype ♂ and 1 ♀ paralectotype *Amblyomma versicolor* (N212) ex *Equus caballus*, Tolosa (22°31′N, 101°22′W), Mexico, 1.X.1907, Mr A. Laughton.

HOSTS & DISTRIBUTION. *A. cajennense* is a common species occurring in abundance on domesticated animals and less frequently from wild hosts. It readily attacks man and has been found naturally infected with the etiologic agent of Rocky Mountain spotted fever, *Rickettsia rickettsii.* The tick ranges from southern Texas in the United States southward to Argentina and the Caribbean islands.

Aponomma draconis Warburton, 1933 : 546, fig. 7

Junior subjective synonym of *Aponomma komodoense* Oudemans, 1928.

NUTTALL 3875. 'Described from 3 ♂♂ and 6 ♂♂ (in poor condition) taken from a "dragon", *Varanus komodoensis,* brought from Komodo Island, Flores, Dutch East Indies, and for some years past in the Zoological Gardens, London. Communicated by Dr P. A. Buxton, April, 1931. Types in Cambridge (N. 3875).'

TYPES. Lectotype ♂ and 2 ♂, 6 ♀ paralectotypes *Aponomma draconis* (N3875) ex *Varanus komodoensis*, brought from Komodo Island (08°36′S, 119°30′E) Indonesia, and for some years past in the Zoological Gardens, London, England, IV.1931. Dr P. A. Buxton.

HOSTS & DISTRIBUTION. *Aponomma komodoense* has been collected on Komodo and nearby Flores Island, Indonesia, on *Varanus komodoensis.* One record of this tick from *Varanus salvator* in Djakarta Zoo was probably a case of accidental parasitism.

Dermacentor imitans Warburton, 1933 : 559, figs 3, 4

NUTTALL 3874. 'Described from 12 ♂ and 1 ♀ taken by Mr W. J. Hamilton, Jun., on a peccary (*Pecari angulatus*) at Turrialba, Costa Rica, on August 1st, 1927, and sent to Cambridge by Prof. R. Matheson. In the same tube were specimens of *Amblyomma mantiquirense.* Types in Cambridge (N.3874).'

TYPES. Lectotype ♂ and 9 ♂, 1 ♀ paralectotypes *Dermacentor imitans* (N 3874), ex *Tayassu tajacu,* Turrialba (09°54′N, 83°41′W), Costa Rica, 1.VIII.1927, W. J. Hamilton, Jr.

HOSTS & DISTRIBUTION. Known also from Panama, Guatemala, and Mexico, *Dermacentor imitans* has been recorded from *Mazama americana* as well as from its common host, the peccary.

Haemaphysalis aciculifer Warburton, 1913 : 125, figs 4, 5

NUTTALL 1981. 'Described from 1 ♂ and 1 ♀ taken, in company with *Rhipicephalus appendiculatus,* from *Cobus thomasi* (an antelope), on the N.E. shore of Lake Edward, Uganda, X. 1911, by S. A. Neave. Types in Entomol. Research Committee's Collection, No. 463 a.'

TYPES. Lectotype ♂ [designated as holotype by Hoogstraal & El Kammah, 1972 : 965], paralectotype ♀ [designated as allotype by Hoogstraal & El Kammah, 1972 : 965] (N1981) ex *Kobus kob thomasi,* N.E. shore of Lake Edward (approx. 00°25′S, 29°30′E), Uganda, X.1911, S. A. Neave [ex Entomological Research Committee 463a] BM NH 1913.8.12: 7–8.

HOSTS & DISTRIBUTION. *Haemaphysalis aciculifer* adults are parasitic on antelopes, domestic cattle, sheep, goats, Cape buffalo, hares and occasionally carnivores that prey upon antelopes and other game. This tick has been recorded from Cameroon, Uganda, Ethiopia, Sudan, Kenya, Tanzania, Zimbabwe, and South Africa. Hoogstraal & El Kammah (1972) gave detailed host and distributional data for *H. aciculifer.*

Haemaphysalis bancrofti Nuttall & Warburton, 1915 : 487, figs 427–430

Junior synonyms: *Haemaphysalis novaeguineae* Krijgsman & Ponto, 1932 : 17; *Haemaphysalis meraukensis* Taylor 1944 : 187; *Haemaphysalis krijgsmani* Kohls 1948 : 157.

NUTTALL 2100, 2114, 2115, 2689, 2691. 'Described from specimens derived from Queensland, Australia: (N. 2100), 2 ♂ and 5 ♀ from *Macropus dorsalis,* Burnett District, III.1913; (N. 2114), 1 ♀ and 1 N, found crawling on collector's trousers, at Brigaton Scrub, Burnett; (N. 2115), 1 ♂, from *Macropus giganteus,* Burnett District, III.1913; (N. 2689), 2 ♀, with eggs and larvae, the ♀s taken from *Macropus dorsalis,* Eidsvold, XII.1913; (N. 2691), 6 ♂, 3 ♀ and 2 N host (?) found at Eidsvold. All collected by Dr T. L. Bancroft, of Eidsvold, after whom the species is named.

Types in Cambridge: (N. 2100, ♂ ♀; N. 2691, N; N. 2689, larvae).

In the following collections (by Nuttall number), Professor Nuttall placed blue type labels—N2100, N2689 (ii) and N2691 (ii). Nuttall 2100 was divided, one vial containing 1 ♂, 1♀ the other vial containing 1 ♂, 4 ♀. In the following collections (by Nuttall number), Professor Nuttall placed blue cotype labels—N2114 (i), (ii), N2115, N2689, N2691.

TYPES. Lectotype ♂ (in vial containing 1 ♂, 1 ♀) and 1 ♂, 5 ♀ paralectotypes *Haemaphysalis bancrofti* (N2100) [1 ♀ vulva on slide] ex *Macropus dorsalis*, Burnett District, Queensland, Australia, III.1913, Dr T. L. Bancroft; paralectotypes 1 ♀ (N2114ii), 1 N (N2114i) crawling on collector's trousers, Brigaton Scrub, Burnett, Queensland, Australia, III.1913, Dr T. L. Bancroft [leg IV of N2114(i) is mounted on a slide] 1 ♂ (N2115) ex *Macropus giganteus,* Burnett District, Queensland, Australia, III.1913, Dr T. L. Bancroft; 2 ♀ (N2689), 223 L (including 7 L mounted on slides) (N2689ii) ex *Macropus dorsalis,* Eidsvold, Queensland, Australia, XII.1913, Dr T. L. Bancroft; 2 N (N2691i), 6 ♂, 3 ♀ (N2691ii), no host cited, Eidsvold, Queensland, Australia, 1913, Dr T. L. Bancroft.

REMARKS. Roberts (1963) cited the original collection data and redescribed the ♂, ♀ and nymph.

HOSTS & DISTRIBUTION. *Haemaphysalis bancrofti* is found in the coastal and subcoastal areas of Queensland and northern New South Wales, Australia, and from Kangaroo Island, South Australia (Roberts, 1970). It is also present in New Guinea. Hosts include a wide range of marsupial mammals as well as most of man's domesticated animals.

Haemaphysalis calcarata houyi Nuttall & Warburton, 1915 : 444

NUTTALL 2996. 'Described from 7 ♂, 1 ♀ and 2 N from Bate, New Cameroon, collected by Dr Houy. Types in the Berlin Museum (No. 279), co-types in Cambridge (N2996).'

TYPES. Lectotype ♂ and 2 ♂, 1 ♀, 1 N paralectotypes *Haemaphysalis houyi* (N2996), host not stated, Bate Cameroun [If the coordinates given by Hoogstraal (1955) are correct, the type locality would now be called Bade, Central African Republic], no date stated, Dr Houy.

REMARKS. Hoogstraal (1954 : 307) raised the taxon to specific rank, then (1955 : 365) reviewed and illustrated *H. houyi* and from information supplied to him from J. Bequaert gave the type locality at approximately 06°40′N, 17°00′E.

HOSTS & DISTRIBUTION. *Haemaphysalis houyi* is known primarily from *Euxerus erythropus* in a narrow belt through Kenya, Uganda and Sudan westward to Senegal.

Haemaphysalis calvus Nuttall & Warburton, 1915 : 445, figs 378, 379

NUTTALL 2120a. 'Described from 3 ♂ and 1 ♀ (N2120a) taken from buffalo, Sekong River, Sandakan, British North Borneo, 19.IV.1913, Dr H. F. Conyngham coll.'

TYPES. Lectotype ♂ and 2 ♂, 1 ♀ paralectotypes (N2120a) ex buffalo, Sekong River, Sandakan (05°50′N, 118°05′E), Sabah, Malaysia, 19.IV.1913, Dr H. F. Conyngham [♀ vulva mounted on a slide].

HOSTS & DISTRIBUTION. *Haemaphysalis calvus* in addition to the original collection has been recorded from *Cervus unicolor*, a tiger, and a bear in Malaysia and Thailand.

Haemaphysalis campanulata Warburton, 1908 : 513, figs 5, 6

NUTTALL 897. Original description 'based on numerous specimens taken from Chinese dogs in Mongolia by Major M. L. Hearn, and received by us from Colonel Skinner in 1906.'

TYPES. Lectotype ♂ and 91 ♂, 5♀ paralectotypes *Haemaphysalis campanulata* (N897) ex Chinese dogs, Mongolia, rec'd 14.X.1906, Major M. L. Hearn.

The above paralectotype total includes 3 ♂, 1 ♀ which were previously pinned and now are retained in a separate vial and 1 ♂, 1 ♀ mounted on a slide.

REMARKS. Nuttall & Warburton (1915) stated, 'Types in Cambridge (N897); we have presented cotypes (♂ ♀) to the British Museum and London School of Tropical Medicine, also (♂) to the Museums in Paris, Berlin, Toulouse (Neumann coll.), and Washington, D.C. (U.S. Dept. Agric.).' [Those USDA specimens consist of 2 ♂, 1 ♀ and are now housed at the Rocky Mountain Laboratories (RML 109832).]

HOSTS & DISTRIBUTION. This species is known from China, Mongolia, Manchuria, Japan and Korea. Hosts include cows, horses, dogs, rats and man.

Haemaphysalis crassa Warburton, 1908 : 516, fig. 8

Junior subjective synonym of *Haemaphysalis punctata* Canestrini & Fanzago, 1878.

BM(NH) 1908.1.14.103–105. 'Description based on two gorged ♀ at the British Museum, in a tube labelled *Haemaphysalis papuana*.'

TYPES. Lectotype ♀ and 1♀ paralectotype *Haemaphysalis crassa* BM(NH) 1908.1.14.103–105, ex. cattle, Zurnabad (40°30′N, 46°15′E), Azerbaijan SSR, USSR.

REMARKS. One of the five vial labels with these ticks bears the following information: '*Haemaphysalis papuana* Thorell ♀, Surnabat Antirinderpest Station, from cattle, Dr E. Dschunkovskii.' Nuttall & Warburton (1915 : 384) spell the locality Surnabad and the collector's name Dschunkowsky.

HOSTS & DISTRIBUTION. *Haemaphysalis punctata* is a parasite on most of man's domesticated animals as well as many species of ground nesting birds. This tick is found throughout central and southern Europe, northern Africa and into the Asiatic areas of Turkey and the USSR.

Haemaphysalis hoodi Warburton & Nuttall, 1909 : 62, figs 7, 8

Junior synonym: *Haemaphysalis africana* Howard, 1909 : 219.

NUTTALL 424. 'Described from numerous specimens of both sexes sent by Dr P. Hood, from Bathurst, Gambia, where it occurred on fowls in May, 1908.'

TYPES. Lectotype ♂ and 14 ♂, 34 ♀ paralectotypes *Haemaphysalis hoodi* (N424) ex fowls, Bathurst, now Banjul (13°28′N, 16°39′W), Gambia, V.1908, Dr P. Hood.

REMARKS. Nuttall & Warburton (1915) p. 486 stated 'Types in Cambridge (N424, adults and N, N1364 N and L); cotypes (♂ ♀ from our collection) at Toulouse.' Specimens in collection

(N1364) mentioned by Nuttall & Warburton (1915) are the types of *Haemaphysalis africana.*

HOSTS & DISTRIBUTION. Distributed throughout the Ethiopian faunal region but perhaps found more in West rather than East Africa, it is exclusively parasitic on birds with a preference for ground dwellers.

Haemaphysalis hoodi orientalis Nuttall & Warburton, 1915 : 486

Junior synonym: *Haemaphysalis zambeziae* Santos Dias 1953 : 1.

NUTTALL 2847, 2848. 'Described from 6 ♂ and 3 ♀ taken from *Procavia manningi* Wroughton, S.W. Shore of Lake Nyasa, British Central Africa, III.1910, S. A. Neave coll. Types in the Imperial Bureau of Entomology coll., London (Nos. 66a and 69); cotypes in Cambridge (N2847 and N2848, 1 ♂, 2 ♀).'

TYPES. Lectotype ♂ and 1 ♂, 1 ♀ paralectotypes *Haemaphysalis hoodi orientalis* (N2847) (Imperial Bureau of Entomology 66a) ex *Heterohyrax brucei manningi,* S.W. Shore, Lake Malawi, Malawi, III.1910, S. A. Neave [♀ vulva mounted on a slide]; BM(NH) 1914.6.15: 1–3; paralectotypes 3 ♂, 2 ♀ (N2848) (Imperial Bureau of Entomology 69), collection data as for (N2847) [1 ♂, 1 ♀ hypostome mounted on a slide].

REMARKS. Hoogstraal (1956 : 161) elevated *H. orientalis* to specific rank.

HOSTS & DISTRIBUTION. *Haemaphysalis orientalis* is a parasite of hyraxes in Malawi, Tanzania, Zambia and Mozambique.

Haemaphysalis howletti Warburton, 1913 : 123, figs 2, 3

NUTTALL 1979. 'Described from 1 ♂ and 1 ♀ taken by F. M. Howlett from a hill pony at Rawalpindi, India (no date). The types are in the Quick Laboratory, Cambridge (N1979).'

TYPES. Lectotype ♂ and 1 ♀ paralectotype *Haemaphysalis howletti* ex hill pony, Rawalpindi (33°36′N, 73°04′E), Pakistan, date not stated on vial label or in Nuttall's catalogue, F. M. Howlett. [♀ vulva mounted on a slide.]

REMARKS. Nuttall & Warburton (1915 : 494) stated the collection date 1912. Dhanda (1964) redescribed the adults and described the immature stages. Nymphs and larvae were collected mostly on rodents and birds. The only adult collected was from a bandicoot. All were from the vicinity of Poona, India.

HOSTS & DISTRIBUTION. *Haemaphysalis howletti* is known from western India, northern Pakistan, and southern Nepal on the above-mentioned hosts.

Haemaphysalis humerosa Warburton & Nuttall, 1909 : 60, figs 4, 5

NUTTALL 669. 'Described from 4 ♂ and 1 ♀ taken from *Perameles macrura,* Barrow Island, N.W. Australia. Presented by Hon. N. C. Rothschild.'

TYPES. Lectotype ♂ and 1 ♂, 1 ♀ paralectotypes *Haemaphysalis humerosa* (N669) (Rothschild 178) ex *Isoodon macrourus,* Barrow Island (20°48′S, 15°23′E), Australia. [♀ vulva mounted on a slide.]

REMARKS. An additional 1 ♂ of this collection was sent to Dr L. O. Howard, U.S. Department of Agriculture, Washington, D.C., 21.V.1909. Nuttall & Warburton (1915) indicated 3 ♂, 1 ♀ and 1 N present in (N669). Roberts (1963) noted that the tube label states 3 ♂ 1 ♀ off *Perameles macrura,* W. Australia. Nuttall has added the note 'one missing from 20.X.1934'.

HOSTS & DISTRIBUTION. *Haemaphysalis humerosa* is collected most frequently from the bandicoot and, in addition to Australia, has been found in New Guinea.

Haemaphysalis inermis aponommoides Warburton, 1913 : 128, fig. 8

NUTTALL 1566. 'Described from numerous ♀'s taken by Colonel F. Raymond F.R.C.V.S., from a Himalayan Zebu at Belgachia, Calcutta, III.1912, in company with *Boophilus australis*. Types in the Quick Laboratory, Cambridge (N1566).'

TYPES. Lectotype ♂ and 19 ♀ paralectotypes *Haemaphysalis inermis aponommoides* (N1566), ex Himalayan Zebu cattle, Belgachia, Calcutta (22°32'N, 88°22'E), India, III.1912, Colonel F. Raymond.

REMARKS. Nuttall & Warburton (1915 : 367) repeated the original description and figures and (p. 549) listed 23 ♀ in the collections of BM(NH), Berlin Museum, and Toulouse. Hoogstraal (1961 : 317) redescribed the female and Hoogstraal (1962 : 195) described the ♂ and raised *aponommoides* to specific rank. The cattle undoubtedly were imported from the north to Calcutta, a city far from this tick's distributional range.

HOSTS & DISTRIBUTION. *Haemaphysalis aponommoides* is known from Nepal, India, Sikkim and China. Adult *H. aponommoides* primarily parasitize artiodactyls but have been found on man, dog, flying squirrel, wildcat and black bear. Immatures have been collected on pheasant and 2 shrew and 4 rodent species (Hoogstraal & Mitchell, 1971).

Haemaphysalis japonica [spelled ***japonnica***] Warburton, 1908 : 512, figs 3, 4

NUTTALL 1247. 'Description based on numerous specimens in a tube labelled *H. flava* at the British Museum . . . Habitat, Japan.'

TYPES. Lectotype ♂ and 1 ♀ paralectotype *Haemaphysalis japonica* (N1247) ex *Capricornis crispus* Hondo (32°27'N, 130°12'E), Kyushu, Japan, received IV.1911 [i.e., received at Cambridge University from Mr A. S. Hirst, BM(NH)], The Duke of Bedford's collector, 6 ♂, paralectotypes data as above, deposited in the BM(NH)—1908.11.7.1–11 (part).

REMARKS. Nuttall & Warburton (1915 : 403) gave the collection data for Warburton's type specimens.

HOSTS & DISTRIBUTION. *Haemaphysalis japonica* is found on dogs, deer, serow, cattle and horses in Japan, Korea, China and Southern Primor, U.S.S.R.

Haemaphysalis japonica douglasi Nuttall & Warburton, 1915 : 403

Junior subjective synonym of *Haemaphysalis japonica* Warburton, 1908.

NUTTALL 1248. 'Described from 4 ♂ taken from *roe-deer*, at Ten-an-fu, Shiensi, Northern China, 19.V.1909, by Captain H. E. M. Douglas. Types in the British Museum and co-types (N.1248 2 ♂) in Cambridge.'

TYPES. Lectotype ♂ *Haemaphysalis japonica douglasi* (N1248) ex *Capreolus capreolus*, Yen-An (36°38'N, 109°27'E), Shensi, Peoples Republic of China, 19.V.1909, Captain H. E. M. Douglas. 7 ♂ paralectotypes, data as above, deposited in the BM(NH)—1911.7.7.28–36.

HOSTS & DISTRIBUTION. See *Haemaphysalis japonica*.

Haemaphysalis koningsbergeri Warburton & Nuttall, 1909 : 65, figs 11, 12

NUTTALL 496. 'Described from 2 ♂ and 2 ♀ sent by Dr J. C. Koningsberger of the Zoological Museum at Buitenzorg, Java, in 1908. Its host was *Felis pardus*.'

TYPES. Lectotype ♂ and 2 ♀ paralectotypes *Haemaphysalis koningsbergeri* (N496) ex *Panthera pardus*, Java, Indonesia, received X.1908. [♀ vulva mounted on a slide].

REMARKS. Nuttall & Warburton (1915 : 467) reduced *H. koningsbergeri* to a synonym of *H. leachi*.

HOSTS & DISTRIBUTION. *Haemaphysalis koningsbergeri* is a parasite of small and medium-size carnivores and found in Vietnam, southern Thailand, Malaysia, Borneo, and on Java and Sumatra in Indonesia.

Haemaphysalis longipalpis Warburton, 1910 : 399, figs 4, 5

Junior subjective synonym of *Haemaphysalis aculeata* Lavarra, 1904.

NUTTALL 1107. 'Described from 10 ♂ and 1 ♀ taken by Mr C. C. Dobell from *Tragulus meminna,* the Mouse Deer, at Colombo, Ceylon, 3.VIII.1909.'

TYPES. Lectotype ♂ and 7 ♂, 1 ♀ paralectotypes *Haemaphysalis longipalpis* (N1107) ex *Tragulus meminna,* Colombo (06°56′N, 79°51′E), Sri Lanka, 3.VIII.1909, C. C. Dobell [♀ vulva mounted on a slide.]

HOSTS & DISTRIBUTION. *Haemaphysalis aculeata* is an uncommon species. Adults are most often collected from the Mouse Deer, immatures have been recorded from *Macaca radiata* and *Paradoxurus zeylonensis.* This tick has been found in Sri Lanka, India and Indonesia.

Haemaphysalis mjöbergi Warburton, 1926 : 57, fig. 3

NUTTALL 3560. 'Described from two specimens in a tube labelled "Rissa equina, Borneo", in a small collection of ticks sent by Dr E. Mjöberg from Sarawak, 7.IV.24.'

TYPES. Lectotype ♂ *Haemaphysalis mjoebergi* (N3560) ex *Cervus unicolor* (probably), Mt Poi, Sarawak, Malaysia, sent 7.IV.1924 by Dr. E. Mjöberg.

REMARKS. Kohls (1961 : 305) noted that 'Rissa' is probably a lapsus for Rusa, a name used for the sambar or red deer, *Cervus unicolor.* He also stated that the second specimen was probably returned to the Sarawak Museum but that it could not be located and may have been lost during the Japanese occupation. The collecting locality of Mt Poi was found in Nuttall's catalogue.

HOSTS & DISTRIBUTION. *Haemaphysalis mjoebergi* has only been collected from *Cervus unicolor* (probably) in Kalimantan, Indonesia, and from grass and fallen leaves at Poi, southwest Sarawak, Malaysia.

Haemaphysalis silacea Robinson, 1912 : 478, fig. 1, a–f

NUTTALL 1629, 2944. 'Described from 4 ♀ found on oxen allowed to run on "starvation camp" from which stock had been excluded for two years, Gonubie Park, East London, South Africa.'

TYPES. Lectotype ♀ and 1 ♀ paralectotype *Haemaphysalis silacea* (N1629), ex cattle, "Starvation Camp", Gonubie Park (32°55′S, 27°59′E), Republic of South Africa, 1911, received from W. F. Cooper [paralectotype ♀ vulva mounted on a slide]; paralectotypes 2 ♀ (N2944), collection data as for (N1629) except date given as 24.II.1911, and collector R. J. Davys.

REMARKS. Nuttall & Warburton (1915 : 418) added the collector's name, Mr R. J. Davys, and the deposition of the types—Cambridge (N1629, N2944). Hoogstraal (1963) reviewed and updated the existing knowledge on *H. silacea.*

HOSTS & DISTRIBUTION. *Haemaphysalis silacea* is known only from South Africa but is no longer found in the type locality. Adults are found most often on cattle but have a comparatively wide host range including sheep, goat, Kudu, hare, mongoose, bushbuck, etc.

Haemaphysalis wellingtoni Nuttall & Warburton, 1908 : 397, figs 9–11

NUTTALL 221. 'Description based on 1 ♂ and 2 ♀ from fowl, Sarawak, Borneo, collected by Dr A. R. Wellington, 1907.'

TYPES. Lectotype ♂ and 10 ♀, 2 N paralectotypes *Haemaphysalis wellingtoni* (N221) ex fowls, Kuching (01°33′N, 110°20′E), Sarawak, I.1907, Dr A. R. Wellington [1 ♀ vulva mounted on a slide.]

REMARKS. Nuttall & Warburton (1915 : 481) stated that 'our description is based on 2 ♂, 11 ♀ and 2 N taken from domestic fowl at Sarawak, Borneo, collected by Dr A. R. Wellington, I.1907.'

HOSTS & DISTRIBUTION. *Haemaphysalis wellingtoni* ranges from Sri Lanka and India through Burma, Thailand, Vietnam, Malaysia, to Borneo and Indonesia. It is a parasite of ground feeding birds and, occasionally, small mammals.

Ixodes ampullaceus Warburton, 1933 : 559, fig. 2

Junior subjective synonym of *Ixodes ugandanus* Neumann, 1906.

NUTTALL 3873. 'Described from 2 ♀ taken by Mr Rupert L. L. Hart on the "edible rat", *Cricetomys ganibicus,* in Uganda.'

TYPES. Lectotype ♀ *Ixodes ampullaceus* (N3873) ex *Cricetomys gambianus,* Kingdom of Ankole (00°30′S, 30°30′E), Uganda, sent 11.III.1931, Mr Rupert L. L. Hart.

REMARKS. Nuttall's catalogue lists only 1 ♀ as being present in this collection rather than the 2 ♀ cited by Warburton in the original collection. The locality of Ankole and the date were also taken from his catalogue.

HOSTS & DISTRIBUTION. *Ixodes ugandanus* is primarily a rodent parasite especially of cane rats in Cameroon, Nigeria, Uganda, Tanzania, Kenya (2 records), Zimbabwe, Mozambique, and South Africa.

Ixodes arvicolae Warburton, 1926 : 56, fig. 2

NUTTALL 3594, 3595. 'Described from four specimens taken by Miss G. E. Pickford and Mr G. E. Hutchinson on water-voles, *Arvicola amphibius amphibius,* at Quy, near Cambridge, in May 1925. One specimen was in company with *I. tenuirostris.* Type at Cambridge.'

TYPES. Lectotype ♀ *Ixodes arvicolae* (N3595) ex *Arvicola terrestris,* Quy (52°13′N, 00°13′E), England, 23.V.1925, Miss G. E. Pickford & Mr G. E. Hutchinson; 2 ♀ paralectotypes *Ixodes arvicolae* (N3594) from nest of *Arvicola terrestris,* Quy (52°13′N, 00°13′E), England, 21–23.V.1925, Miss G. E. Pickford & Mr G. E. Hutchinson.

REMARKS. In Nuttall's catalogue, N3594 is labelled 3 ♀ cotypes [one of which is now missing] and N3595 is labelled type. *Ixodes arvicolae* is possibly a junior synonym of *Ixodes apronophorus* Schulze, 1924.

HOSTS & DISTRIBUTION. In addition to the type host, *I. arvicolae* has been collected on the coypu, *Myocastor coypus.* The tick is known from Cambridgeshire and Kent, England.

Ixodes caledonicus Nuttall, 1910 : 408, figs 1–3

NUTTALL 961, 1142, 1200. 'Described from 1 ♀ (N961) on rocks below a dove's nest, Fastcastle, Scotland, 6.IX.1909 by Dr J. H. Ashworth (Edinburgh); 1 N and 3 L (N1142) found on a young pigeon, from a dovecot [sic], at Duniface [sic], Stirlingshire, Scotland, 18.IV.1910 and 1 ♀ and 4 N (N1200) from the same source, 9.VIII.1910, communicated by Mr Williams Evans (Edinburgh).'

TYPES. Lectotype ♀ *Ixodes caledonicus* (N961) rocks below dove's nest, Fastcastle (55°56′N, 02°14′W), Scotland 6.IX.1909, Dr J. H. Ashworth [Nuttall & Warburton (1911) state J. F. Cormack and J. Waterston as collectors]; paralectotypes 3 L (N1142), 2 N (N1200) ex *Columba livia,* Dunipace (56°01′N, 03°55′W), Stirlingshire, Scotland 18.IV.1910, W. Evans.

REMARKS. Nuttall & Warburton (1911 : 346) indicated that 1 ♀, N, L were deposited in Cambridge and 1 ♀, N, L were deposited in Edinburgh. The specimens deposited in Edinburgh are now missing.

HOSTS & DISTRIBUTION. *Ixodes caledonicus* is an avian ectoparasite and ranges from Scotland to Norway, Denmark, and Germany.

Ixodes cavipalpus Nuttall & Warburton, 1908 : 394, figs 1–5

NUTTALL 245. 'Description based on 2 ♂ and 7 ♀ from a baboon (*Cynocephalus babuin*), Kansanshi, N.W. Rhodesia, collected by Dr A. Yale Massey.'

TYPES. Lectotype ♂ and 3 ♀ paralectotypes (in alcohol) 1 ♂, 1 ♀ (each mounted on a slide) *Ixodes cavipalpus* (N245), ex *Papio cynocephalus,* Kansanshi (12°05′S, 26°25′E), Zambia, sent 22.I.1907 to London School of Hygiene and Tropical Medicine, Dr A. Yale Massey [A slide is present containing 1 ♂, 1 ♀ spiracular plate.]

REMARKS. Massey's (1908) mention of the name *Ixodes cavipalpus* was a nomen nudum. Nuttall & Warburton (1911) add the collection date I.1907.

HOSTS & DISTRIBUTION. *Ixodes cavipalpus* is found on a wide range of hosts including primates, carnivores, and lagomorphs but is found most often on the Artiodactyla. This tick ranges from Cameroun in West Africa, eastward through Zaire, Uganda, Kenya, and southward through Tanzania, Malawi, Zambia, Angola, Zimbabwe, Mozambique into the northern Transvaal of South Africa.

Ixodes dentatus spinipalpis Hadwen & Nuttall *in* Nuttall, 1916 : 301, figs 6–8

NUTTALL 3180, 3181: 'My description is based on (N. 3180) 1 ♀ found on *Lepus americanus,* 1.IX.1910, (N. 3181) 3 N found on *L. americanus, Sciurus hudsonius douglasii* and upon a *child* respectively, besides 4 larvae (17 were originally collected) from *Lepus americanus,* 5.III.1910, all taken at Mount Lehman, British Columbia, Canada, by Dr S. Hadwen. Types in Cambridge.'

TYPES. Lectotype ♀ *Ixodes dentatus spinipalpis* (N3180) ex *Lepus americanus,* Mount Lehman (49°07′N, 122°23′W) British Columbia, Canada, 1.IX.1910, Dr Semour A. Hadwen; 2 N, 4 L paralectotypes *Ixodes dentatus spinipalpis* [1 N ex *Homo sapiens*; 1 N ex *Lepus americanus*; 4 L (1 L mounted on a slide) ex *Lepus americanus*], Mount Lehman (49°07′N, 122°23′W), British Columbia, Canada, 5.III.1910, Dr Semour A. Hadwen.

REMARKS. The nymph from *Tamiasciurus hudsonicus* could not be located and is not mentioned in Nuttall's catalogue of ticks. Cooley & Kohls (1942 : 1734) raised *I. spinipalpis* to specific rank.

HOSTS & DISTRIBUTION. Adults and immatures of *Ixodes spinipalpis* are found on numerous species of lagomorphs and rodents. Immatures are also found on birds. The tick is found in the Pacific and Rocky Mountain areas of the U.S.A. and in British Columbia and Alberta, Canada.

Ixodes eichhorni Nuttall, 1916 : 295, figs 1, 2

NUTTALL 2672, 2675. 'Described from a ♀ found on the *collector's person* at Rook Island, Friedrich Wilhelmshaven, German New Guinea, IX.1913 and several unfed N's found on a *Kingfisher*, Manus, Admiralty Islands, IX–X.1913 by Mr A. F. Eichhorn after whom the species is named and to whom I am indebted for the specimens. Considering the part of the world they come from and the remarkable agreement in structure between the ♀ and N I attribute them to one species although they were collected from different hosts. The only species hitherto known to possess circular anal grooves is *I. rasus* Neumann, 1899, from

Africa, which differs from *I. eichhorni* in numerous respects, the coxae being unarmed and trenchant, etc. The types (N. 2672, 2675) are in Cambridge.'

TYPES. Lectotype ♀ *Ixodes eichhorni* (N2672) ex *Homo sapiens,* Rook Island, now known as Umboi Island (05°36′S, 148°00′E), Papua New Guinea, IX.1913, Mr A. F. Eichhorn; 2 N paralectotypes *Ixodes eichhorni* (N2675), ex Kingfisher, Manaus Island (02°05′S, 147°00′E), Admiralty Islands.

HOSTS & DISTRIBUTION. *Ixodes eichhorni* is a parasite of birds in Papua New Guinea, New Hebrides, Admiralty Islands, and Western Samoa.

Ixodes fecialis aegrifossus Warburton & Nuttall, 1909 : 250.

Junior subjective synonym of *Ixodes fecialis* Warburton & Nuttall, 1909.

NUTTALL 339. 'Described from three mutilated ♀s taken from an *Opossum,* Tamborine Mountain, Logan River, S. E. Queensland, April, 1907, and labelled "Scrub-ticks," sent by Professor R. T. Hewlett (London) who received them from the Bacteriological Institute, Brisbane.'

TYPES. Lectotype ♀ and 1 ♀ paralectotype *Ixodes fecialis aegrifossus* (N339) ex Opossum, Tamberine Mountain, Logan River (27°43′S, 153°18′E), Queensland, Australia, IV.1907, sent by Professor R. T. Hewlett (London) who received them from the Bacteriological Institute, Brisbane, Australia.

HOSTS & DISTRIBUTION. *Ixodes fecialis* is found on a wide range of both small and large marsupials as well as mice, rats, and occasionally man. It is found in Victoria, Tasmania, New South Wales, Queensland and Western Australia.

Ixodes gigas Warburton, 1910 : 397, figs 1, 2

Junior subjective synonym of *Ixodes acutitarsus* (Karsch, 1880).

NUTTALL 1104. 'Described from two specimens in the India Museum, Calcutta (no. 5992/10 and no. ?) taken at Punkabani, Darjiling District, E. Himalayas (no host recorded).'

TYPES. Lectotype ♂ *Ixodes gigas* (N1104), host unknown, Punkabani, Darjeeling District (27°02′N, 88°16′E), India; 1 ♂ paralectotype with same data deposited in the Indian Museum, Calcutta (5992/10).

REMARKS. In Nuttall's catalogue of ticks the collecting locality is spelled Punkabari.

HOSTS & DISTRIBUTION. *Ixodes acutitarsus* will parasitize most medium to large sized wild and domestic animals and often man and has been recorded from India, Nepal, Peoples Republic of China (Tibet), Burma, Japan, and Taiwan.

Ixodes kelloggi Nuttall & Warburton, 1908 : 396, figs 6–8

Junior subjective synonym of *Ixodes brunneus* Koch, 1844.

NUTTALL 278, 279, 280. 'Description based on 3 ♀, one from a thrush (from Palo Alto, Cal. 1895), one from *Cyancitta* [sic] *stelleri frontalis* (R. C. Snodgrass, coll. 1895, California), and a third from a bird (probably California), sent by Prof. V. L. Kellogg of Stanford University in 1907. (In alcohol.)'

TYPES. Lectotype ♀ *Ixodes kelloggi* (N280) ex Thrush, Palo Alto (37°21′N, 122°07′W), California, U.S.A., 14.XI.1895; 1 ♀ [slide mounted capitulum] paralectotype *Ixodes kelloggi* (N279) ex *Cyanocitta stelleri*, California, U.S.A. 15.XII.1895, R. E. Snodgrass.

REMARKS. Exact dates for (N280) and (N279) are taken from Nuttall's catalogue. The specimen from a bird, probably California (N278) is missing.

HOSTS & DISTRIBUTION. *Ixodes brunneus* is exclusively a parasite of birds usually infesting migratory species. With the exception of one record from Venezuela, valid records of *I. brunneus* have only been from the United States. For a listing of the 21 states from which it has been collected see Keirans & Clifford (1978 : 54).

Ixodes kempi Nuttall, 1913 : 131 fig. 1

Junior subjective synonym of *Ixodes granulatus* Supino, 1897.

NUTTALL 2066. 'Described from eight partly gorged ♀s, found on *Sciurus erythraceus intermedius,* at Kobo (400 feet elevation), India, Abor Expedition, by S. W. Kemp, 29.III.1912. (Indian Museum, Calcutta, No. 1247/17.)'

TYPES. Lectotype ♀ and 2 ♀ paralectotypes *Ixodes kempi* (N2066) ex *Callosciurus erythraeus intermedius*, Kobo (27°47′N, 95°23′E), India (altitude 122 m), 24.III.1912, S. W. Kemp.

REMARKS. The date of 24.III.1912 is in Nuttall's catalogue and on the vial label with the ticks.

HOSTS & DISTRIBUTION. *Ixodes granulatus* is primarily a rodent parasite in Nepal, India, Vietnam, Thailand, Burma, Cambodia, Indonesia, Philippines, Malaysia, Japan, Korea, China, and Taiwan.

Ixodes loricatus spinosus Nuttall, 1910 : 411, fig. 4

[Preoccupied by ***spinosus*** Neumann, 1899]

Junior subjective synonym of *Ixodes luciae* Senevet, 1940.

NUTTALL 647: 'Described from (N647) 3 ♀'s taken from a large Opossum, Tabasco de la Frontera, Mexico, in the month of May (ex Hon. N. C. Rothschild's collection).'

TYPES. Lectotype ♀ and 1 ♀ paralectotype *Ixodes loricatus spinosus* (N647) ex *Didelphis* sp., Frontera (18°32′N, 92°38′W), Tabasco, Mexico, May, ex Hon. N. C. Rothschild's collection.

HOSTS & DISTRIBUTION. Adults of *Ixodes luciae* prefer opposums as hosts but immatures are more often found on rodents. The tick is found from southern Mexico to Peru, Bolivia and Brazil with one record from Argentina.

Ixodes oldi Nuttall, 1913 : 135, fig. 3

NUTTALL 2065. 'Described from 14 slightly engorged ♀'s found on a bush-cat, at Komatendu, Sierra Leone, West Africa, by J. J. Simpson, 13.VIII.1912 (Imperial Bureau of Entomology, No. 604).'

TYPES. Lectotype ♀ and 5 ♀ paralectotypes *Ixodes oldi* (N2065) ex bush cat (probably a West African species of *Genetta*), Komatendu, Sierra Leone (locality not verified), 13.VIII.1912, J. J. Simpson.

REMARKS. Nuttall (1913) states 14 ♀ in the original collection. In his tick catalogue, however, he recorded 7 ♀ in collection (N2065). Arthur (1958 : 47) and (1965 : 138) discusses a 'holotype ♀' deposited in the BM(NH) bearing the above original data. However, as can be seen from Nuttall's statement, he did not select a holotype.

HOSTS & DISTRIBUTION. *Ixodes oldi* is primarily a parasite of carnivores, especially genets, although it is also found on the insectivore, *Crocidura* sp. It ranges from Sierra Leone in the west, eastward to Tanzania and south to the Republic of South Africa.

Ixodes percavatus rothschildi Nuttall & Warburton, 1911 : 221

NUTTALL 634. 'Described from (N634) 2 ♀'s and 3 N taken from a puffin (ex Rothschild Coll., no locality recorded).'

TYPES. Lectotype ♀ and 1 ♀, 2 N paralectotypes *Ixodes rothschildi* (N634) (Rothschild 159) ex *Fratercula arctica*, no other data.

REMARKS. Zumpt (1952 : 17) and independently Arthur (1953 : 222) gave specific rank to *I. rothschildi*. Arthur (1963 : 134) referred to 2 ♀, 3 N in the type series. One nymph is now missing.

HOSTS & DISTRIBUTION. *Ixodes rothschildi* is a parasite of marine birds in the coastal areas of Great Britain, Ireland, and France.

Ixodes ricinoides Nuttall, 1913 : 136, fig. 4

[Preoccupied by ***ricinoides*** De Geer, 1778]

Ixodes nuttallianus Schulze, 1930 nom. nov.

NUTTALL 1401, 1402. 'Described from five partially fed ♀s; one ♀ found on a *swamp deer*, Wen-chwan-hsien, near Si-ho-hsien, China, and four ♀s found on *musk deer* (same locality). The specimens, obtained by purchase from Mr T. V. Sherrin, Taxidermist, Hampton, Middlesex, are in Cambridge. (N. 1401, 1402).'

TYPES. Lectotype ♀ *Ixodes ricinoides* (N1401) ex *Hydropotes inermis*, Wen-Ch'uan (44°59′N, 81°04′E), Sinkiang Province, Peoples Republic of China 1.VII.1911, purchased from Mr T. V. Sherrin; 3 ♀ paralectotypes *Ixodes ricinoides* (N1402) ex *Mochus moschiferus*, Wen-Ch'uan (44°59′N, 81°04′E), Sinkiang Province, Peoples Republic of China, 1.VII.1911, purchased from Mr T. V. Sherrin.

REMARKS. Collection dates were taken from Nuttall's Catalogue of Ticks.

HOSTS & DISTRIBUTION. In addition to the members of the Cervidae mentioned above, *I. nuttallianus* has also been collected from the barking deer, *Muntiacus muntjak*. It has been found also on *Capricornis sumatraensis, Naemorhedus goral*, dog, goat, cattle and zhum [hybrid cow-yak]. *Ixodes nuttallianus* is distributed from Sinkiang Province, China, through Tibet and Nepal. For a detailed discussion of *I. nuttallianus* see Clifford *et al.* (1971).

Ixodes ricinus gibbosus Nuttall, 1916 : 300, fig. 5

NUTTALL 2553. 'Described from (N2553) 5 ♂, 6 ♀ found by Mr W. H. J. van Heemstra on *Capra hircus*, Smyrna, Asiatic Turkey, XI.1913, in company with *Hyalomma aegyptium* and *Haemaphysalis cinnabarina* var. *punctata*. Types in Cambridge.'

TYPES. Lectotype ♂ and 4 ♂, 6 ♀ paralectotypes *Ixodes ricinus gibbosus* (N2553) ex domestic goat, Izmir (38°25′N, 27°09′E), Turkey, XI.1913, Mr W. H. J. van Heemstra.

REMARKS. Saratsiotis (1970 : 661) raised *I. gibbosus* to specific rank.

HOSTS & DISTRIBUTION. *Ixodes gibbosus* infests, cattle, sheep, goats, horses and camels. *Ixodes gibbosus* replaces *I. ricinus* in the drier biotopes of Italy, Greece, Yugoslavia, Albania, Bulgaria, Cyprus, Turkey, and Israel.

Ixodes victoriensis Nuttall, 1916, 297, fig. 3

NUTTALL 3194. 'Described from 2 gorged ♀'s from wombat (doubtless *Phascolomys mitchelli*), Victoria, Australia, X.1892, received from Dr Georgina Sweet . . . Types in the collection of Dr Sweet (No. 236a), Melbourne, Australia, and (N. 3194) in Cambridge.'

TYPES. Lectotype ♀ *Ixodes victoriensis* (N3194) from wombat (doubtless *Vombatus ursinus*) Victoria, Australia, X.1892, received from Dr Georgina Sweet.

REMARKS. The ♀ specimen in the collection of Dr Sweet (No. 236a) is now missing.

HOSTS & DISTRIBUTION. *Ixodes victoriensis* has been collected only from wombats in Victoria, Australia.

Rhipicentor bicornis Nuttall & Warburton, 1908 : 399, figs 12–16

NUTTALL 320f. 'Description based on 3 ♂ and 1 ♀ collected by Dr Old in North Nyassa, British Central Africa. Host not stated (preserved in 5% formalin, then in spirit).'

TYPES. Lectotype ♂ and 2 ♂ [1 ♂ in alcohol, 1 ♂ mounted on two slides, i.e., capitulum, body] paralectotypes *Rhipicentor bicornis* (N320f), host unknown, Malawi, III.1907, Dr J. E. S. Old.

REMARKS. The 1 ♀ *Rhipicentor bicornis* is missing.

HOSTS & DISTRIBUTION. *Rhipicentor bicornis* has been collected on cattle, goats, jackal, eland, dogs, lions, and several other hosts in Zaire, Ruanda, Burundi, Angola, Zambia, Malawi, Zimbabwe, and Namibia.

Rhipicephalus coriaceus Nuttall & Warburton, 1908 : 402, figs 17–20

Junior subjective synonym of *Rhipicephalus supertritus* Neumann, 1907.

NUTTALL 320e. 'Description based on 2 ♂ and 6 ♀ collected in North Nyassa, British Central Africa, by Dr Old, 1907; 1 ♂ (the larger) from Benguella, W. Africa, collected by Dr F. C. Wellman, 1907. Hosts not stated. (Preserved in 4% formalin, transferred to spirit.)'

TYPES. Lectotype ♀ and 1 ♂, 2 ♀ [1 ♀ mounted on a slide] paralectotypes *Rhipicephalus coriaceus* (N320e) host unknown, Malawi, III.1907, Dr J. E. S. Old; 1 ♂ paralectotype *Rhipicephalus coriaceus* (N320e), Distrito de Benguela (12°00′S, 15°00′E), Angola, 1907, Dr F. Creighton Wellman.

REMARKS. The paralectotype ♀ in alcohol has had its genital aperture removed and mounted on a slide. A photograph of this structure appeared in Feldman-Muhsam (1956 : pl. III, fig. 11).

HOSTS & DISTRIBUTION. *Rhipicephalus supertritus* adults have been collected on Carnivora-*Panthera leo,* Perissodactyla-*Diceros bicornis* and *Equus burchelli* and many species of Artiodactyla. The tick ranges from Sudan, Zaire, Tanzania, Angola, Zambia, and Malawi to Mozambique.

Rhipicephalus evertsi albigeniculatus Nuttall & Warburton, 1916 : 327

Junior subjective synonym of *Rhipicephalus evertsi mimeticus* Dönitz, 1910.

NUTTALL 1619, 1650c, 1694b: 'Received by us from the Lower Congo, only differs from the above [reddish yellow legs] in having banded legs.'

TYPES. Lectotype ♂ and 15 ♂, 8 ♀ paralectotypes *Rhipicephalus evertsi albigeniculatus* (N1650c) ex cattle, Mateba Island (05°54′S, 12°50′E), Zaire, 23–30.IV.1912. Received from Professor Meuleman (Brussels); 5 ♂, 3 ♀ paralectotypes *Rhipicephalus evertsi albigeniculatus* (N1694b) ex cattle Mateba Island (05°54′S, 12°50′E), Zaire, received 22.VI.1912; 2 ♂ paralectotypes *Rhipicephalus evertsi albigeniculatus* (N1619) ex cattle, Kasonga either (05°28′S, 21°11′E) or (05°42′S, 18°48′E), Zaire, Drs Dutton & Todd.

HOSTS & DISTRIBUTION. *Rhipicephalus e. mimeticus* parasitizes cattle, horses, sheep, goats, and a few of the larger wild hosts such as zebras and antelope. It occurs in drier areas of southern Africa and can be found together with *R. e. evertsi* in the savannahs of northern Angola and southwestern Zaire.

Rhipicephalus longiceps Warburton, 1912 : 11, figs 6, 7

NUTTALL 351, 393. 'Described from 18 ♂s and 3 ♀s (No. 351) from "Klipspringer Bok" taken by Dr F. C. Wellman in 1907 in the Benguella Hinterland, Angola, long. E.15°05′ lat. 12°44′, altitude 1360 metres, and 19 ♂s and 2 ♀s. (No. 393) in a mixed collection of ticks taken by the same collector in the same district during 1908 but with no host recorded. Types in Cambridge.'

TYPES. Lectotype ♂ and 17 ♂, 2 ♀ (1 ♂ abnormal) paralectotypes *Rhipicephalus longiceps* (N351), ex *Oreotragus oreotragus*, Benguela (12°35′S, 13°25′E), Angola, received 3.XII.1907, sent by Dr F. Creighton Wellman [♀ vulva mounted on a slide]; paralectotypes 15 ♂, 2 ♀ (N393), host not stated, Benguela (12°35′S, 13°25′E), Angola, 3.V.1908, Dr F. Creighton Wellman.

REMARKS. The one abnormal ♂ from N351 was described and figured by Nuttall (1914 : 253). Santos Dias (1958) examined the type-material of this species and stated that it consisted of: 12 ♂♂ and 1 ♀ (*Types*), from a 'Klipspringer bok' (*Oreotragus* sp.), Benguela, by Dr F. C. Wellman, 30/12/1907—No. 351, ex-Nuttall collection; 12 ♂♂ and 1 ♀ (*Cotypes*), by the same collector (3/5/1908), at the same locality and host—No. 393, ex-Nuttall collection.

HOSTS & DISTRIBUTION. *Rhipicephalus longiceps* is a rare tick known only from Angola and Southwest Africa (Namibia) and parasitic upon kudu and klipspringer bok.

Rhipicephalus masseyi Nuttall & Warburton, 1908 : 404, figs 21–26

NUTTALL 246. 'Description based on 31 ♂ and 21 ♀ from *Bos caffer*, Kansanshi, N.W. Rhodesia, collected by Dr A. Yale Massey, 1907 (preserved in spirit).'

TYPES. Lectotype ♂ and a total of 21 ♂, 13 ♀ paralectotypes [19 ♂, 10 ♀ in alcohol, 1 ♂, 2 ♀, chelicerae mounted on slides plus 1 ♂, 1 ♀ in alcohol deposited in the BM(NH) collection—1906.11.6.11–12] *Rhipicephalus masseyi* (N246) ex *Syncerus caffer*, Kansanshi (12°05′S, 26°25′E), Zambia, 1907, Dr A. Yale Massey [1 ♀ vulva mounted on a slide].

HOSTS & DISTRIBUTION. Adult *Rhipicephalus masseyi* have been collected from *Atilax paludinosus, Phacochoerus aethiopicus, Potamochoerus porcus, Tragelaphus angasi, T. scriptus*, and *Syncerus caffer* in Rwanda, Zaire, Tanzania (southern), Angola, Zambia and Mozambique.

Rhipicephalus neavei Warburton, 1912 : 7, figs 2, 3

Junior subjective synonym of *Rhipicephalus kochi* Dönitz, 1905.

NUTTALL 1414. 'The specimens which appeared most characteristic and were selected as types were taken by Mr S. A. Neave from an eland near the mouth of the Tasangazi R., Luangwe Valley, N.E. Rhodesia [E.R.C. No. 168]. Types at British Museum and Cambridge.'

TYPES. Lectotype ♂ and 3 ♂, 4 ♀ paralectotypes *Rhipicephalus neavei* (N1414) ex *Taurotragus oryx* near mouth of the Lusangazi River (13°25′S, 31°34′E), Luangwa Valley, Eastern Province, Zambia, 1.IX.1910, Mr S. A. Neave; 14 ♂, 6 ♀ paralectotypes, collection data as above, deposited in the BM(NH) collection (Reg. No. 1911.12.5.16–40).

REMARKS. Santos Dias (1958 : 478) cited this collection as containing 1 ♂, 1 ♀.

HOSTS & DISTRIBUTION. Adults of *Rhipicephalus kochi* are found on medium to large-size mammals in central and eastern Africa and as far south as Zambia.

Rhipicephalus neavei var. ***punctatus*** Warburton 1912 : 10, figs 4, 5

NUTTALL 1411. 'Described from 13 ♂s and 8 ♀s from Kudu, near Fort Mlangeni, Central

Angoniland, Nyasaland (Neave, V.1910, E.R.C. No. 132), 1 ♀ from *Impala aepiciros melampur* (sic) on N.-W. shore of L. Nyasa (Neave, VII.1910, E.R.C. No. 127), and 1 ♀ from reed-buck, Valley of Rukuru R., N. Nyasaland (Neave, 26.VI.1910, E.R.C. No. 158) . . . Types at British Museum and Cambridge.'

TYPES. Lectotype ♂ and 1 ♂, 1 ♀ paralectotypes *Rhipicephalus neavei punctatus* (N1411) ex *Tragelaphus strepsiceros*, near Fort Mlangeni (14°41′S, 34°32′E), Ncheu District, Malawi, V.1910, S. A. Neave; 11 ♂, 4 ♀ paralectotypes, collection data as above, deposited in the BM(NH) collection (Reg. No. 1911.12.5.41–50).

REMARKS. Santos Dias (1951 : 373) raised *Rhipicephalus punctatus* to specific status.

HOSTS & DISTRIBUTION. Host predilections and distributional data for *Rhipicephalus punctatus* in Africa are very poorly known because so few collections of this species have been accurately identified.

Rhipicephalus sculptus Warburton, 1912 : 13, figs 8, 9

NUTTALL 1409, 1448. 'Described from 11 ♂s and 5 ♀s (E.R.C. No. 230a) [This is Nuttall 1448] from roan antelope, Mpalali R., Marimba, Nyasaland (Old, I.1911) . . . 1 ♂ (E.R.C. No. 227a) [This collection is now missing] from the same locality and host . . . 3 ♂ and 1 ♀ (No. 115b) [This is Nuttall 1409] from zebra, S. Rukura Valley, N. Nyasaland (Neave, VI.1910) . . . Types at the British Museum and Cambridge.'

TYPES. Lectotype ♂ and 1 ♀ paralectotype *Rhipicephalus sculptus* (N1409), ex *Equus burchelli,* locality possibly South Rukuru River (10°44′S, 34°14′E), Malawi, VI.1910, S. A. Neave; paralectotypes 2 ♂, data as above, deposited in the BM(NH) collection. Reg. no. 1911.12.5.53–54; paralectotypes 3 ♂, 2 ♀ (N1448) ex *Hippotragus equinus,* locality possibly Mpala River, now known as Mipala River (15°55′S, 35°16′E), Malawi, 1.I.1911, Dr J. E. S. Old [♀ vulva mounted on a slide].

REMARKS. Santos Dias (1958 : 479) indicated 1 ♂ 1 ♀ present in N1409 and 3 ♂ 2 ♀ present in N1448. Although he did not mention the latter Nuttall number, he listed all relevant collection data.

HOSTS & DISTRIBUTION. *Rhipicephalus sculptus* is a rare species known only from the zebra and a few members of the Artiodactyla in eastern and southern Africa.

Rhipicephalus simpsoni Nuttall, 1910 : 413, figs 6, 7

NUTTALL 1214. 'Described from 5 ♂'s and 11 ♀'s found on a large rodent, Oshogbo, S. Nigeria, W. Africa, 28.II.1910, J. J. Simpson (N1214). (41b, Entomological Research Committee for Tropical Africa).'

TYPES. Lectotype ♂ and 1 ♂, 1 ♀ paralectotypes *Rhipicephalus simpsoni* (N1214), ex *Thryonomys* sp. (probably), Oshogbo (07°46′N, 04°34′E), Nigeria, 28.II.1910, J. J. Simpson [♀ vulva mounted on a slide]. Paralectotypes 1 ♂, 4 ♀ *Rhipicephalus simpsoni*, data as above, deposited in the BM(NH) collection Reg. no. 1911.5.10.6.12.

REMARKS. Santos Dias (1958) indicated 2 ♂, 1 ♀ *R. simpsoni* present in Nuttall 1214 when he examined the Nuttall collection in 1955.

HOSTS & DISTRIBUTION. *Rhipicephalus simpsoni* is a specific parasite of cane rats, *Thryonomys* spp. and is widely distributed in the Ethiopian faunal region.

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Appendix I

Holotypes and previously selected lectotypes of tick species described by Nuttall, Warburton, Cooper, and Robinson

Nuttall Collection Number	Original Name	Senior Subjective Synonym	Type Status and Depository
1106	*Amblyomma annandalei* Warburton, 1910: 403, fig. 8	*A. supinoi* Neumann, 1905	Holotype ♀ BM(NH) Nuttall Coll.
*None	*Amblyomma crassum* Robinson, 1926 : 177, fig. 83	–	Holotype ♀ BM(NH) reg. No. 1926.7.27.1
3615	*Amblyomma dammermani* Warburton, 1927 : 409, pl. XXVII, fig. 3	*A. cyprium* Neumann, 1899	Holotype ♀ BM(NH) Nuttall Coll.
2940	*Amblyomma longirostrum* Cooper & Robinson, 1908 : 457, figs 1–5	*A. humerale* C. L. Koch 1844	Holotype ♀ Depository unknown
565	*Amblyomma quasicyprium* Robinson, 1926 : 237, fig. 117	*A. cyprium* Neumann, 1899	Holotype ♀ Depository unknown
2943	*Aponomma quadratum* Cooper & Robinson, 1908 : 468, figs 22–24	*A. varanensis* Supino, 1897	Holotype ♂ BM(NH) Nuttall Coll.
2942	*Aponomma simplex* Cooper & Robinson, 1908 : 466, figs 18–21	*A. fimbriatum* C. L. Koch, 1844	Holotype ♂ BM(NH) Nuttall Coll.
515a	*Haemaphysalis bispinosa intermedia* Warburton & Nuttall, 1909 : 69, fig. 16	–	Lectotype ♀ Hoogstraal & Trapido (1963) BM(NH) Nuttall Coll.
1108	*Haemaphysalis cuspidata* Warburton, 1910 : 401, figs 6, 7	–	Lectotype ♂ Trapido (1965) BM(NH) Nuttall Coll.
693a	*Haemaphysalis dentipalpis* Warburton & Nuttall, 1909 : 67, fig. 14	*H. asiaticus* (Supino, 1897)	Lectotype ♂ Hoogstraal & Trapido, (1966) BM(NH) Nuttall Coll.
635	*Haemaphysalis doenitzi* Warburton & Nuttall, 1909 : 64, figs 9, 10	–	Lectotype ♀ Hoogstraal & Wassef (1973) BM(NH) Nuttall Coll.

Appendix I continued

Nuttall Collection Number	Original Name	Senior Subjective Synonym	Type Status and Depository
1997	*Haemaphysalis kinneari* Warburton, 1913 : 127, fig. 6	–	Holotype ♀ BM(NH) Nuttall Coll.
760, 761, 762	*Haemaphysalis montgomeryi* Nuttall, 1912 : 57, figs 7, 8	–	Lectotype ♂ (N760) Hoogstraal *et al.* (1966) BM(NH) Nuttall Coll.
540c	*Haemaphysalis proxima* Warburton & Nuttall, 1909 : 61, fig. 6	*H. cornigera* Neumann, 1897	Holotype ♀ BM(NH) Nuttall Coll.
1647	*Haemaphysalis spiniceps* Warburton & Nuttall, 1909 : 68, fig. 15	*H. cornigera* Neumann, 1897	Holotype ♂ BM(NH) Nuttall Coll.
3614	*Haemaphysalis toxopei* Warburton, 1927 : 407, fig. 3	–	Lectotype ♂ Hoogstraal (1964) BM(NH) Nuttall Coll.
1648	*Haemaphysalis vidua* Warburton & Nuttall, 1909 : 66, fig. 13	–	Holotype ♂ BM(NH) Nuttall Coll.
1400	*Haemaphysalis warburtoni* Nuttall, 1912 : 55, figs 5, 6	–	Lectotype ♂ Hoogstraal (1966) BM(NH) Nuttall Coll.
1219	*Hyalomma monstrosum* Nuttall & Warburton, 1908 : 414, figs 41–45	–	Holotype ♂ Depository unknown
*None	*Ixodes daveyi* Nuttall, 1913 : 133, fig. 2	–	Holotype ♀ BM(NH) reg. No. 1913.8.12.6
650	*Ixodes fecialis* Warburton & Nuttall, 1909 : 58, figs 1, 2	–	Holotype ♀ BM(NH) Nuttall Coll.
*None	*Ixodes nairobiensis* Nuttall, 1916 : 299, fig. 4	–	Holotype ♀ BM(NH) reg. No. 1915.10.14.1
3872	*Ixodes petauristae* Warburton, 1933 : 558, fig. 1	–	Holotype ♀ BM(NH) Nuttall Coll.
3581	*Ixodes theodori* Warburton, 1927 : 405, fig. 2	*I. acuminatus* Neumann, 1901	Holotype ♀ BM(NH) Nuttall Coll.
1103	*Rhipicephalus breviceps* Warburton, 1910 : 398, fig. 3	*R. sanguineus* (Latreille, 1806)	Holotype ♀ BM(NH) Nuttall Coll.

*Specimens donated to the British Museum (Natural History) by Nuttall *et al.* or described from material in the Museum collections.

Appendix II

Types of tick species described by Nuttall, Warburton, Cooper, and Robinson which are not contained in the collections of the British Museum (Natural History)

Species	Location	Comments
Aponomma javanense Cooper & Robinson, 1908	Unknown	'Description based on 3 ♀'s.'
Aponomma gervaisi lucasi Warburton, 1910	ZSI, Calcutta	–
Haemaphysalis aborensis Warburton, 1913	ZSI, Calcutta	–
Haemaphysalis cornigera anomala Warburton, 1913	ZSI, Calcutta	–
Haemaphysalis leachi indica Warburton, 1910	ZSI, Calcutta	–
Haemaphysalis turturis Nuttall & Warburton, 1915	MNHU, Berlin	–
Ixodes neumanni Nuttall & Warburton, 1911	ENV, Toulouse	–
Ornithodoros asperus Warburton, 1918	MNHU, Berlin	–
Ornithodoros nattereri Warburton, 1927	NM, Wien	–
Rhipicentor nuttalli Cooper & Robinson, 1908	Unknown	'Description based on a single ♂.'
Rhipicephalus phthirioides Cooper & Robinson, 1907	Unknown	'Description based on two dried ticks . . . a male and a female . . .'

ZSI, Calcutta = Zoological Survey of India, Calcutta (formerly Indian Museum, Calcutta).
MNHU, Berlin = Museum für Naturkunde der Humboldt-Universität, Berlin, D.D.R.
ENV, Toulouse = L'École Nationale Vétérinaire de Toulouse, France.
NM, Wien = Naturhistorisches Museum, Wien, Austria.

A revision of the spider genus *Hispo* (Araneae: Salticidae)

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Introduction

Unlike most genera of the spider family Salticidae, *Hispo* Simon, 1886 can be easily recognized by the characteristic form of the carapace and the presence of a constriction behind the posterior median eyes. The genus is represented in both the Oriental and Ethiopian regions and at present includes 11 known species. Several of these were originally described in the genera *Astaenochestes* Simon, 1900 or *Pseudomarengo* Caporiacco, 1947. The later genus was revised by Roewer (1965), however, they are here considered to be synonymous with *Hispo*.

In this paper, the species are divided into two species groups which may be readily separated by the presence or absence of a fovea. The species included in both groups are morphologically similar and in most cases they can be distinguished from one another by the structure of the genitalia, particularly the form of the palpal tibial apophyses in males. The presence or absence of white hairs on the clypeus and the occurrence of furrows or striae on the anterior surface of the chelicerae provide useful characters for separating otherwise similar species. The degree of variation cannot be adequatey demonstrated for most species as the genus is not well represented in museum collections. The biology is virtually unknown, some species live in woodland or forest litter and could be considered ant-like, but there is no behavioural evidence to suggest a mimetic relationship with ants.

The measurements were made in the manner described by Wanless (1978*a*).

Genus ***HISPO*** Simon

Hispo Simon, 1886 : 393. Type species *Hispo cingulata* Simon, by monotypy. Simon, 1901 : 449, 451, 452; 1903*a* : 1050. Petrunkevitch, 1928 : 186. Roewer, 1954 : 985. Bonnet, 1957 : 2219. Wanless (1981).

Astaenorchestes Simon, 1900 : 397. Type species *Astaenorchestes frenatus* Simon, by original designation and monotypy. Simon, 1901 : 450–452. Petrunkevitch, 1928 : 185. Roewer, 1954 : 985. Bonnet, 1955 : 766. **Syn. n.**

Pseudomarengo Caporiacco, 1947 : 228. Type species *Pseudomarengo inermis* Caporiacco, by original designation. Roewer, 1954 : 951; 1965 : 32. **Syn. n.**

Although Roewer (1954) and Bonnet (1957) give the year 1885 as the publication date for the genus *Hispo*, the date of publication given on the title page is 'avril 1886'. The confusion arose because the part concerned was issued for the year 1885.

DEFINITION. Small to large spiders ranging from about 3·5 to 8 mm in length. Sexual dimorphism not marked. Distinctive colour markings sometimes present; not hirsute. *Carapace*: very low to moderately high; constricted behind posterior median eyes and usually with two shallow depressions behind anterior medians; fovea present or absent; microsculpturing variable, cuticle sometimes iridescent. *Eyes*: anteriors contiguous, apices level or slightly procurved; posterior median eyes relatively small, closer to anterior laterals than to posterior laterals; posterior row usually narrower than anterior row with a space between the posterior lateral eyes and the lateral margins of the carapace; quadrangle length between 39 and 50 per cent of carapace length. *Clypeus*: very low to low. *Chelicerae*: small to medium, more or less vertical, anterior surface irregularly strigose or smooth, sometimes

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with a 'scooped-out' furrow on each chelicera; promargin with 4–6 contiguous teeth, retromarginal teeth similar, but minute more numerous (4–10) and forming a serrated ridge. *Maxillae*: parallel to subparallel, blades more or less rounded. *Labium*: tongue-shaped, about as long as broad or broader than long. *Sternum*: elongate scutiform, sometimes attenuate anteriorly. *Pedicel*: short. *Abdomen*: elongate; scuta absent; spinnerets subequal in length, anteriors and posteriors unequally robust, medians slender; colulus apparently lacking; traecheal system (Fig. 5C) (one species examined), arising from transverse slit immediately in front of anterior spinnerets, apparently simply branched and limited to abdomen. *Legs*: moderately long and slender, I and sometimes II enlarged or elongate; fringes usually lacking, spines weak to moderately strong, usually more numerous on posterior legs; claws generally pectinate (difficult to see in most species), tufts present, usually a stiff curved setae lying between claws on legs I–II; scopulae rarely present. *Female palp*: moderately long and slender. *Male palp* (Fig. 1A, B): with branched tibial apophysis, occasionally with small ventral apophysis; cymbium sometimes depressed and sclerotized basally; embolus (e) usually robust, long and curved originating centrally or subapically; conductor (c) a modified part of the embolic shaft, rarely present (Fig. 11A, B); tegulum (t) pleated, and folded distally, the resulting lobe, when present, resembling an apophysis (l) (Fig. 7F); median apophysis (m) small, slender with a distal hook, often difficult to see in lateral view; subtegulum (st) not pleated, seminal reservoir dark, usually indistinct. *Epigyne* Fig. 5G, J): opening paired, indistinct with sclerotized margins; introductory ducts (f) paired, proximally translucent with glandular 'appendixes' (c), distally dark and coiled around the tube connecting the primary and secondary spermathecae; spermathecae dumb-bell-shaped, primary spermathecae (p) small with leaf-like fertilization ducts; secondary spermathecae (s) small to large and globular, on distal margin a lobe-like structure (r) which resembles the stretcher found in some linyphiid spiders.

REMARKS. The epigyne structure of *Hispo bipartita* Simon clearly differs from that described above, but the vulva has not been examined as only one adult female is available for study. In any event the generic placement of *H. bipartita* will have to be reviewed when the related genera *Massagris* Simon, and *Tomocyrba* Simon are revised.

AFFINITIES. *Hispo* is closly related to the genera *Massagris* and *Tomocyrba*, both of which have foveae and a constriction behind the posterior median eyes which are positioned much closer to the anterior laterals than to the posterior laterals. The male palps of *Hispo* although distinctive, show morphological similarities to these genera in the form of the tegulum and median apophysis. It is possible that the *bipartita*-group of *Hispo* may have to be transferred into *Massagris* as the genitalia would appear to be rather similar.

It will also be necessary to re-examine some of the amber salticids described by Petrunkevitch (1942, 1958). The fossil genus *Gorgopsina* Petrunkevitch, is evidently close to *Tomocyrba* and the type species of *Gorgopsina, G. frenata* (Koch & Berendt) may well prove to be synonymous with recent *Tomocyrba*.

Wanless (1978*b*) suggested that the simple tracheal system found in species of *Portia* Karsch indicated a relationship with lyssomanid spiders. However, as *Hispo* does not appear to have any close affinities with known lyssomanid spiders, while possessing a simple tracheal system (Fig. 5C), this proposition will need to be reconsidered when more genera have been examined.

DIAGNOSIS. The *cingulata*-group of species of *Hispo* can be easily distinguished from the genera *Massagris* and *Tomocyrba* by the absence of a fovea. The *bipartita*-group can be distinguished by the very low carapace.

BIOGEOGRAPHY. The present distribution of *Hispo* can suggest historically different patterns of dispersal depending in which period of geological time the genus evolved and the present species came into being. As most species have been described from Madagascar it seems plausable to suggest that *Hispo* evolved in the Malagasy region. If this happened before the disruption of Gondwanaland then vicariance may be responsible for the occurrence of only

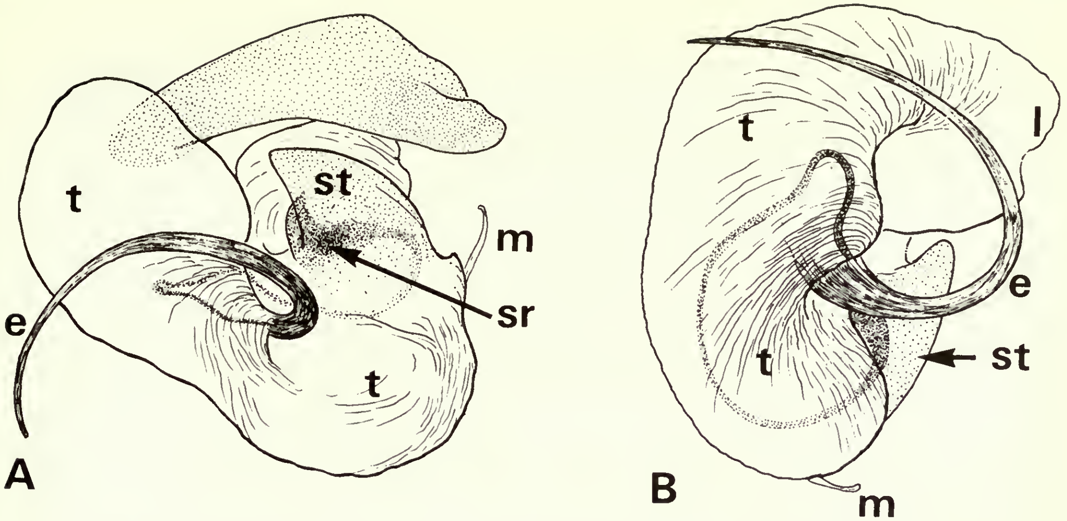

Fig. 1 *Hispo striolata* Simon, ♂, expanded palp: A, lateral view; B, ventral view.

one species in Africa (*H. inermis* (Caporiacco)) and two species in the Seychelles (*H. alboclypea* Wanless and *H. striolata* Simon). It is worth noting that although the Seychellois species are closely related to each other, *H. alboclypea* is evidently closer to *H. inermis,* while *H. striolata,* is closer to *H. pullata* sp. n. from Madagascar. These four species comprise the *striolata*-subgroup which is hopefully of monophyletic origin.

If on the other hand these species reached Africa and the Seychelles after the disruption of Gondwanaland we should not postulate a relict distribution but rather a recent one which may have occurred as a result of aerial dispersal, i.e. ballooning or some other mechanism such as rafting. Platnick (1976) has suggested that vicariance is responsible for most intercontinental distribution patterns in spiders and that the role of ballooning, at least for medium-sized and large ground-dwelling species has been greatly exaggerated. Some salticids are known to balloon as adults, and no doubt, ballooning plays an important role in their distribution particularly at a regional level. Howevever, Platnick is probably correct in his basic hypothesis and we may be sure that some distribution patterns in the Salticidae are the result of vicariance.

If vicariance is responsible for the present distribution patterns in *Hispo* then species can be expected to occur in the Comoro Islands and India. Unfortunately the occurrence of *H. bipartita* in India and Sri Lanka does not fulfil the prediction for as mentioned above, this species may have to be transferred into *Massagris,* and its distribution reconsidered when that genus is revised.

List of species in the genus *Hispo* Simon, 1886

Hispo alboclypea Wanless (1981)
H. alboguttata Simon, 1903
H. bipartita Simon, 1903
H. cingulata Simon, 1886
H. frenata (Simon, 1900)
H. inermis (Caporiacco, 1947)
H. macfarlanei sp. n.
H. pullata sp. n.
H. striolata Simon, 1897
H. sulcata sp. n.
H. tenuis sp. n.

Key to species of *Hispo*

1	Fovea lacking; sternum truncate anteriorly (Figs 2C, 10D)	***cingulata*-group**	2
–	Fovea present; sternum attenuate anteriorly (Fig. 12B)	***bipartita*-group**	15
2	Males		3
–	Females		11
3	Palpal conductor present (Fig. 11A, B) (Madagascar)	***cingulata*** Simon (p. 193)	
–	Palpal conductor absent		4
4	Tibial apophysis with backward pointed spur (Fig. 9J, K) (Madagascar)	***macfarlanei*** sp. n. (p. 191)	
–	Tibial apophysis without backward pointed spur		5
5	Clypeus clothed in white hairs		6
–	Clypeus not white haired		7
6	Embolus large and robust (Fig. 2E) (Madagascar)	***pullata*** sp. n. (p. 183)	
–	Embolus small and slender (Fig. 4A) (Seychelles)	***alboclypea*** Wanless (p. 185)	
7	Embolus very robust (Fig. 7F); dorsal prong of tibial apophysis with small prolateral spur (Fig. 7G) (Madagascar)	***tenuis*** sp. n. (p. 189)	
–	Embolus otherwise; dorsal prong of tibial apophysis without a prolateral spur		8
8	Anterior surface of chelicera with a distinct furrow (Fig. 6E, 8F) (Madagascar)		9
–	Furrow lacking; anterior surface of chelicerae irregularly strigose		10
9	Lateral prong of tibial apophysis with a small spur (Fig. 8B, C)	***sulcata*** sp. n. (p. 190)	
–	Lateral prong of tibial apophysis without a spur (Fig. 6C)	***frenata*** (Simon) (p. 188)	
10	Legs I swollen (Fig. 5E); embolus slender (Fig. 5H) (Africa)	***inermis*** (Caporiacco) (p. 186)	
–	Legs I elongate (Fig. 3C); embolus robust (Fig. 3A) (Seychelles)	***striolata*** Simon (p. 184)	
11	Clypeus clothed in white hairs		12
–	Clypeus not white haired		14
12	Epigynal opening with median scape-like projection (Fig. 9C) (Madagascar)	***macfarlanei*** sp. n. (p. 191)	
–	Epigynal opening without median scape-like projection		13
13	Epigynal openings subcontiguous, transversely elongate, lateral margins extending beyond secondary spermathecae (Figs 10F, 11C, D) (Madagascar)	***cingulata*** Simon (p. 193)	
–	Epigynal openings separate, obliquely elongate, lateral margins not extending beyond secondary spermathecae (Fig. 4B) (Seychelles)	***alboclypea*** Wanless (p. 185)	
14	Carapace with depressions behind anterior median eyes; epigynal openings subcontiguous (Fig. 3D) (Seychelles)	***striolata*** Simon (p. 184)	
–	Carapace without depressions behind anterior median eyes; epigynal openings separate (Fig. 5F, I) (Africa)	***inermis*** (Caporiacco) (p. 186)	
15	Abdomen with discoidal white and black markings (Fig. 13A) [species only known from a subadult ♀] (Sumatra)	***alboguttata*** Simon (p. 196)	
–	Discoidal markings lacking; epigyne with large openings and tangled fertilization ducts near posterior margin (Fig. 12F) (India, Sri Lanka)	***bipartita*** Simon (p. 195)	

The ***cingulata*-group**

The *cingulata*-group is comprised of nine known species, one from Africa, two from the Seychelles and six from Madagascar, which can be readily distinguished from species of the *bipartita*-group by the absence of a fovea.

Within this group two subgroups based on the structure of the male palp can be recognized. In the *striolata*-subgroup (*H. striolata* Simon, *H. alboclypea* Wanless, *H. inermis* (Caporiacco) and *H. pullatta* sp. n.), the dorsal prong of the palpal tibial apophysis is relatively small and unmodified. In the *cingulata*-subgroup (*H. cingulata* Simon, *H. frenata* (Simon), *H. tenuis* sp. n., *H. sulcata* sp. n., and *H. macfarlanei* sp. n.), the tibial apophysis is relatively large and often provided with spurs. *H. cingulata* is further distinguished by having a modified embolic shaft.

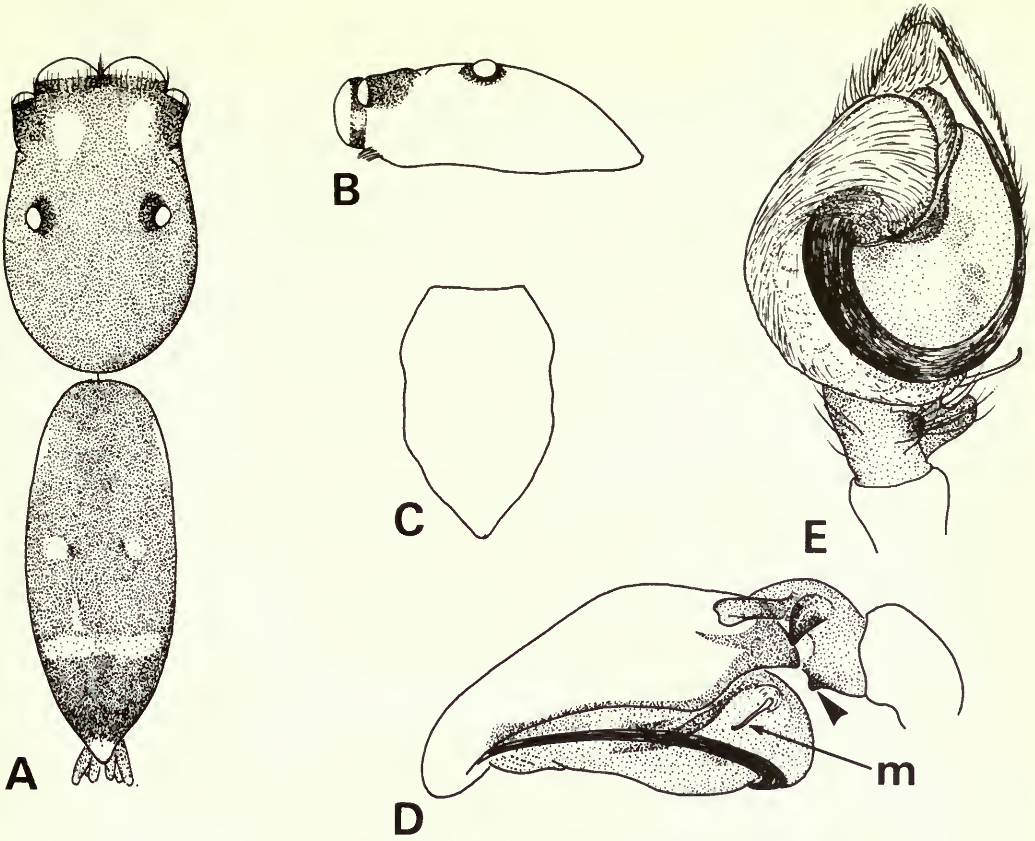

Fig. 2 *Hispo pullata* sp. n., holotype ♂: A, dorsal view; B, carapace, lateral view; C, sternum; D, palp, lateral view; E, palp, ventral view.

Hispo pullata sp. n.
(Fig. 2A–E)

Diagnosis. *Hispo pullata* is closely related to *H. striolata* Simon, but can be separated by the presence of a fringe of white hairs on the clypeus.

Female. Unknown.

Male holotype. *Carapace* (Fig. 2A, B): finely rugose to finely punctate-reticulate within quadrangle; brownish orange, weakly iridescent. *Eyes*: with black surrounds; anteriors contiguous, apices slightly procurved, sparsely fringed in light brown hairs. *Clypeus*: fringed in white hairs. *Chelicerae*: with fine irregular striae; brownish orange, weakly iridescent; teeth not examined. *Maxillae and labium*: brownish orange. *Sternum* (Fig. 2C): light orange, shiny. *Abdomen*: yellow-brown lightly tinged black with indistinct whitish markings clothed in white hairs; anal tubercle whitish. *Legs*: legs I heaviest, dark brown; other legs light brown to yellow-brown. Spination of legs I: metatarsi with 1 proventral spine, tibiae with 1 distal proventral, femora with 3 dorsal and 1 distal prolateral spine; other leg spines weak, but more numerous especially on legs III–IV. *Palp* (Fig. 2D, E): similar to that of *H. striolata,* but the embolus is slightly more robust and the ventral apophysis of the tibia a little more pronounced.

Dimensions (mm): total length 3·84; carapace length 1·76, breadth 1·16, height 0·72; abdomen length 2·12; eyes, anterior row 1·12, middle row 0·88, posterior row 0·92; quadrangle length 0·86. *Ratios*: AM : AL : PM : PL :: 10·5 : 4·5 : 1 : 4, AL–PM–PL :: 5–9.

VARIATION. ♂ total length 3·3 to 4·1 mm, carapace length 1·56—1·88 mm (4 specimens).

DISTRIBUTION. Madagascar.

MATERIAL EXAMINED. Madagascar: Beanana, holotype ♂, ii. 1970 (*A. Lambillon,* MT. 142.600) (MRAC, Tervuren). Antongil, paratypes 3 ♂♂, (*A. Mocqueries*) (MNHN, Paris. 12759).

Hispo striolata Simon
(Figs 1A–B; 3A–F)

Hispo striolata Simon, 1897 : 387, ♂, ♀. Lectotype ♂, Seychelles (MNHN, Paris, 11409) [Examined]. Simon, 1901 : 450, 451. Hirst, 1911 : 382. Roewer, 1954 : 985. Bonnet, 1957 : 2220. Prószyński, 1971 : 417. Wanless, (1981) [Lectotype designated].

DIAGNOSIS. *Hispo striolata* is closely allied to *H. pullata* sp. n., but can be distinguished by the absence of a fringe of white hairs on the clypeus. The female of *H. pullata* is unknown.

REMARKS. This species has recently been redescribed in a faunistic study on Salticidae from

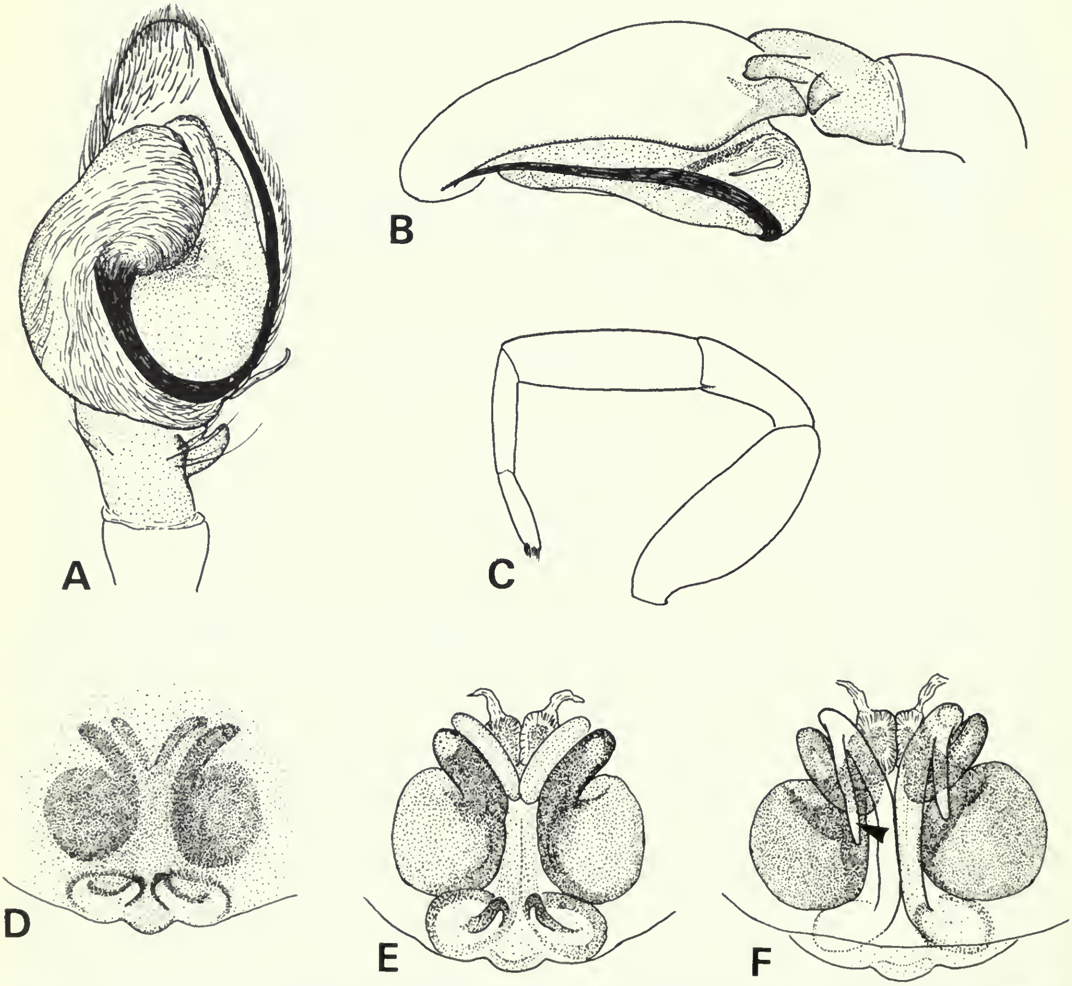

Fig. 3. *Hispo striolata* Simon, ♂: A, palp, ventral view; B, palp, lateral view; C, leg I. ♀: D, epigyne; E, vulva, ventral view; F, vulva, dorsal view.

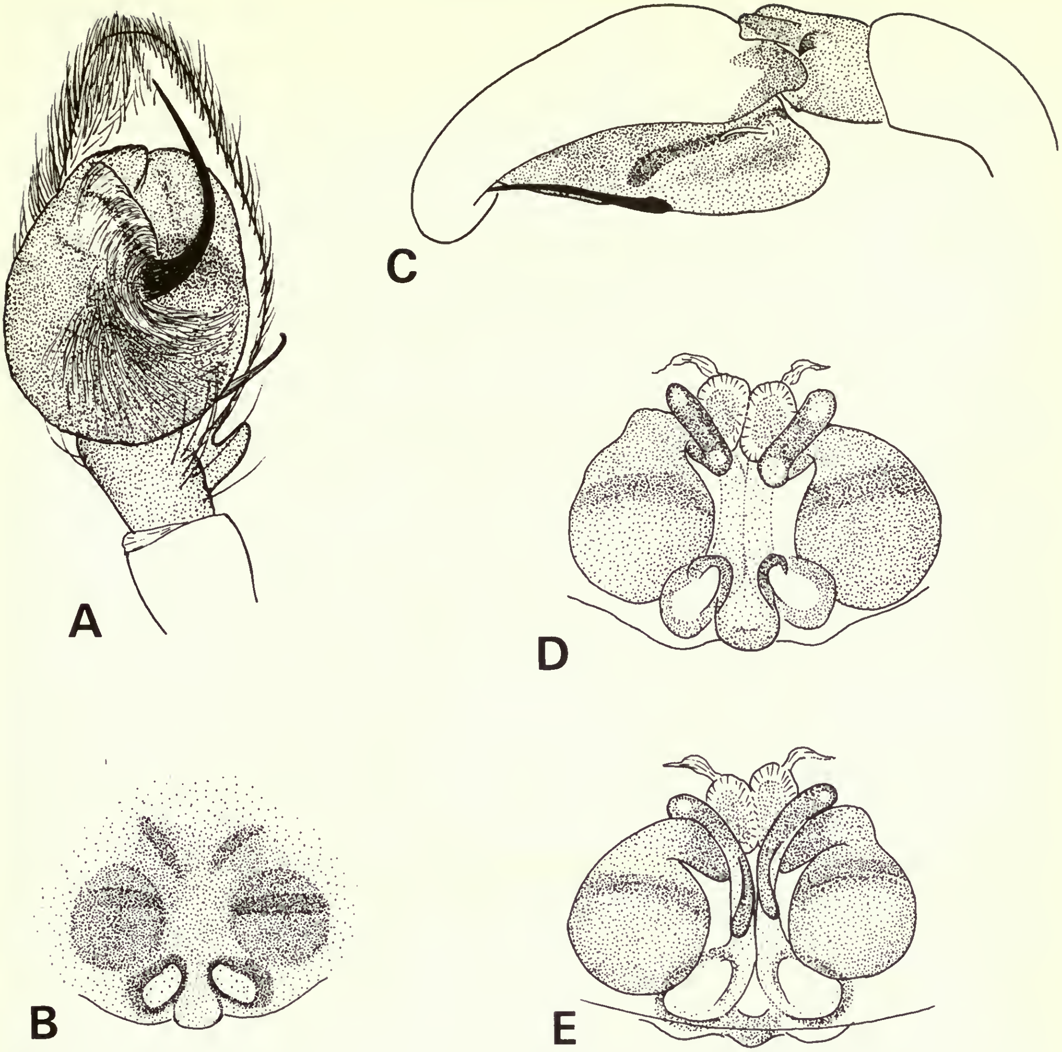

Fig. 4 *Hispo alboclypea* Wanless, ♂: A, palp, ventral view; C, palp, lateral view. ♀: B, epigyne; D, vulva, ventral view; E, vulva, dorsal view.

the Seychelle Islands (Wanless, 1981) but, for completeness, I have provided figures of the genitalia.

DISTRIBUTION. Seychelle Islands: Mahé, Silhouette, Praslin.

MATERIAL EXAMINED. 9 ♂♂, 3 ♀♀, including the lectotype; for data see Wanless (1981).

Hispo alboclypea Wanless
(Fig. 4A–E)

Hispo alboclypea Wanless (1981), ♂, ♀. Holotype ♂, allotype ♀, Seychelles, Silhouette, (BMNH. 1952.12.17.210–214) [Examined].

DIAGNOSIS. *H. alboclypea* is closely related to *H. inermis* (Caporiacco) but can be readily distinguished by the presence of a fringe of white hairs on the clypeus and the structure of the genitalia (Fig. 4A–E).

Remarks. This species has only recently been described (Wanless, 1981) and as in the case of *H. striolata,* only figures of the genitalia are provided.

Distribution. Seychelle Islands: Mahé, Silhouette.

Material examined. 4 ♂♂, 2♀♀, including the holotype; for data see Wanless (1981).

Hispo inermis (Caporiacco) comb. nov.
(Fig. 5A–J)

Pseudomarengo inermis Caporiacco, 1947 : 228, ♂. Holotype ♂, Kenya, Lac Dijpe (TM, Budapest) [Examined]. Roewer, 1954 : 951 : 1965 : 33.

Pseudomarengo rufescens Caporiacco, 1947 : 229, ♀. Holotype ♀, Kenya, Moshi (TM, Budapest) [Examined]. Roewer, 1954 : 951; 1965 : 33 [=*P. inermis*].

Diagnosis. *Hispo inermis* is closely related to *H. alboclypea* Wanless, but can be readily separated by the absence of a fringe of white hairs on the clypeus and the structure of the genitalia (Fig. 5D, F–J).

Male from Angola. *Carapace* (Fig. 5A, B): punctured-reticulate, weakly iridescent especially within quadrangle; depressions behind AM hardly apparent; dark orange-brown with faint sooty markings; thinly clothed in fine pale brown hairs. *Eyes*: with black surrounds; anteriors contiguous, apices slightly procurved, sparsely fringed in whitish hairs. *Clypeus*: edged black with scattered pale brown hairs. *Chelicerae*: with fine irregular striae; dark brown, shiny; teeth not examined. *Maxillae*: orange-brown, inner distal margins whitish. *Labium*: slightly broader than long; orange-brown. *Sternum*: elongate scutiform; orange tinged black, shiny. *Abdomen*: mottled yellow-brown and black with vague transverse bands of whitish lanceolate hairs; spinnerets blackish. *Legs*: legs I (Fig. 5E) and II robust; legs I dark orange-brown with tarsi yellow-brown, shiny with a violet tinge under some angles of illumination, venter of tibiae and patellae scantily fringed in brown hairs; other legs brownish yellow lightly tinged black. Spines few and weak, apparently lacking on legs I–I. *Palp* (Fig. 5D, H): ventral tibial setae relatively stout; embolus slender partly hidden by the subtegulum in ventral view.

Dimensions (mm): total length 3·08; carapace length 1·56, breadth 1·03, height 0·47; abdomen 1·56; eyes, anterior row 0·84, middle row 0·8, posterior row 0·82; quadrangle length 0·64. *Ratios*: AM : AL : PM : PL :: 8 : 3·5 : 1 : 3·5, AL–PM–PL :: 3·2—6·5.

Female from Angola. Similar to ♂ except for the following. *Carapace*: finely punctate-reticulate, weakly iridescent especially in eye region; dark orange, thinly clothed in fine pale orange hairs. *Chelicerae*: small, light orange, shiny; promargin with 3 teeth, retromargin with 5 or 6 forming a serrated ridge. *Sternum*: pale yellow-orange with darker margins. *Abdomen*: whitish yellow clothed in fine pale brown hairs. *Legs*: more or less as in ♂, but pale yellow orange with scanty scopulae on tarsi IV (♂ similar, but scopulae less noticeable). *Epigyne* (Fig. 5G, I, J): in this specimen the broken off embolus tip (e) can be seen in the left opening.

Dimensions (mm): total length 4·56; carapace length 1·88, breadth 1·26, height 0·60; abdomen length 2·84; eyes, anterior row 1·04, middle row 0·94, posterior row 1·04; quadrangle length 0·8. *Ratios*: AM : AL : PM : PL :: 9·2 : 4·2 : 1 : 4, AL–PM–PL :: 4·5–8·5.

Variation. ♂ total length 3·0 to 4·2 mm, carapace length 1·36–1·88 mm (8 specimens). ♀ total length 3·9 to 5·2 mm, carapace length 1·64–1·88 mm (9 specimens). Depth of colour varies from yellow-brown to brown-black, but this could be the effects of preservation. The epigynes are sometimes plugged and the number of coils visible through the integument varies; there are usually three on each side (Fig. 5F), but evidently the coils can overlap so that in some specimens only two are apparent (Fig. 5I).

Distribution. Angola, Botswana, Kenya, Zaire.

Material examined. Angola: Dundo, R. Luachimo, 1 ♂, 25.11.1948 (*A. de Barros* Machado, Ang. 400.26); Dundo, in house, 1 ♂, v.1960 (*A. de Barros Machado,* Ang. 14938);

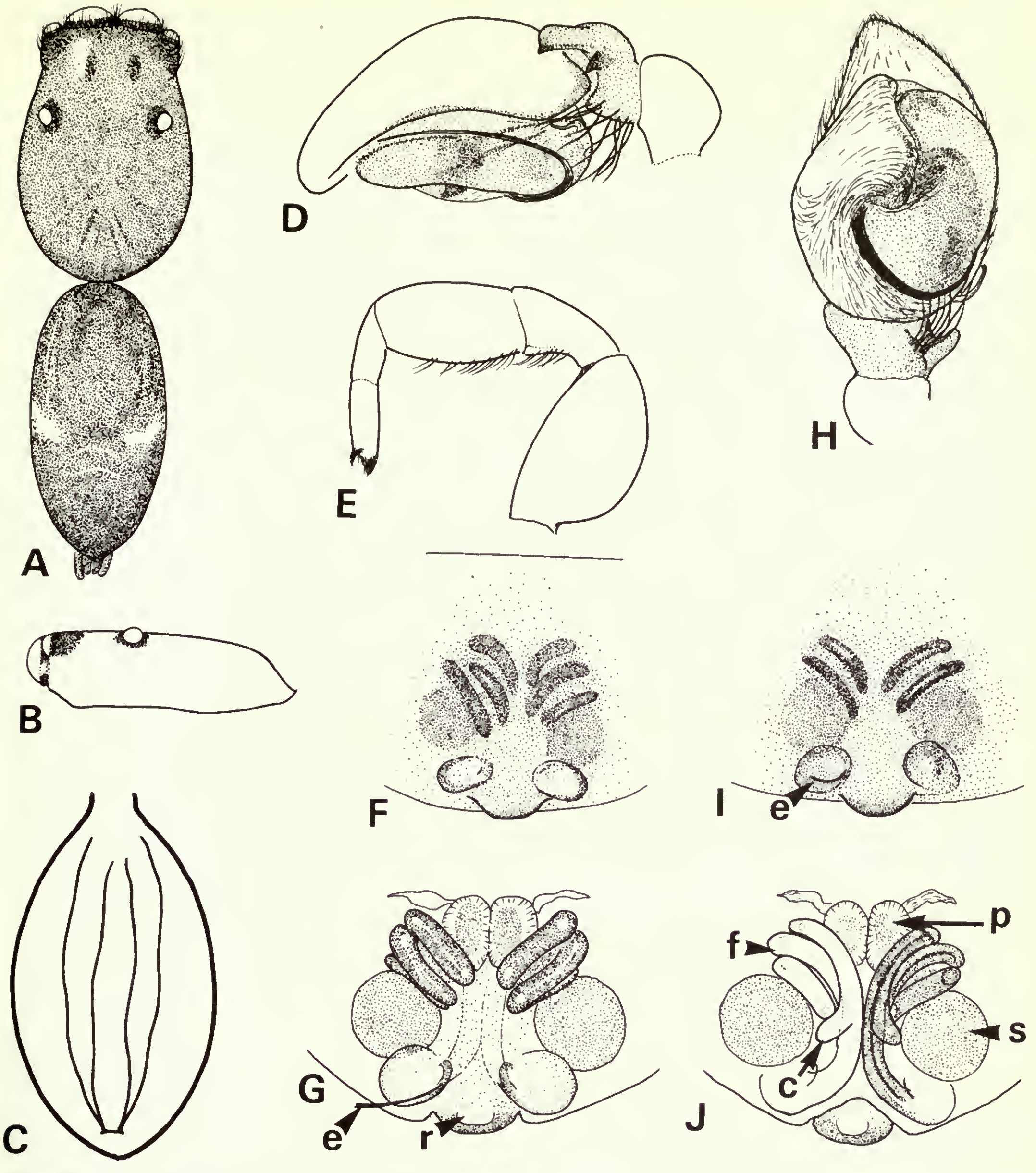

Fig. 5 *Hispo inermis* (Caporiacco), ♂: A, dorsal view; B, carapace, lateral view; D, palp, lateral view; E, leg I; H, palp, ventral view. ♀: C, tracheal system, schematic; F, epigyne; G, vulva, ventral view; I, epigyne, another specimen; J, vulva, dorsal view.

Dundo, forest gallery nr. museum, 2 ♂♂, 8 ♀♀, iii.1948 (*A. de Barros Machado,* Ang. 414.5); Tchivinguiro, forest litter, 1 ♂, 27.ix.1949 *(A. de Barros Machado,* Ang. 1877.21). Botswana: Maqwee, Mopane woodland, pitfall trap, 1 ♂, 12.xii.1975 (*A. Russel-Smith)* (BMNH). Kenya: Lac Djipe, holotype ♂ [*Pseudomarengo inermis*], x.1904 (*K. Kittenberger,* 1228/1905) (TM, Budapest); Moshi, holotype ♀ [*P. rufescens*], ix.1903 (*K. Kittenberger,* 1228/1906) (TM, Budapest). Zaire: lac Tanganika, Ile de Mboko, humus, 1 ♀, 6.ii.1957 (*N. Leleup*, MT. 91383); Kivu, Terr. Uvira, massif de l'Itombwejtête de source riv. Kalimabenge, forêt de montagne avec bambous, 2900 m, 1 ♀, xii.1958 (*N. Leleup*, MT. 113194); Kwango, Terr. Feshi, forêt de tete de la source Sengi, dans humus, 1 ♀, iii.1959 (*N.*

Leleup, MT. 113785); Tshuapa, Bamania, 1 ♂, xii.1954 (*P. Hulstaert*, MT. 84034) (MRAC. Tervuren).

Hispo frenata (Simon) comb. nov.
(Fig. 6A–G)

Astaenorchestes frenatus Simon, 1900 : 397, ♂. LECTOTYPE ♂ (here designated) Madagascar (MNHN, Paris, 13127) [Examined]. Simon, 1901 : 450–452. Roewer, 1954 : 985. Bonnet, 1955 : 766. Prószyński, 1971 : 379.

DIAGNOSIS. *Hispo frenata* is closely related to *H. tenuis* sp. n., *H. sulcata* sp. n., and *H. macfarlanei* sp. n., but can be separated by the absence of spurs on the palpal tibial apophyses (Fig. 6C).

FEMALE. Unknown.

MALE LECTOTYPE (in poor condition). *Carapace* (Fig. 6A, D): brown-black, an iridescent sheen within quadrangle; scattered white hairs below lateral eyes (badly rubbed). *Eyes*: with black surrounds; anteriors more or less contiguous, apices slightly procurved, sparsely fringed in white hairs. *Clypeus*: rubbed, but probably sparsely fringed in light brown hairs. *Chelicerae* (Fig. 6E): smooth with deep cross furrows; brown-black, rather shiny; promargin with 4 teeth, retromargin with 6 or 7 forming a serrated ridge. *Maxillae and labium*: brown-black. *Sternum* (Fig. 6F): grey-yellow, shiny. *Abdomen*: moderately elongate; brown tinged black, original pattern lost, but irregular spots of whitish hair present. *Legs*: legs I longest, brown-black with yellow-brown tarsi, thinly clothed in fine pale orange hairs; other legs yellow-brown tinged black. Spination of legs I: tibiae with 2 distal ventral spines;

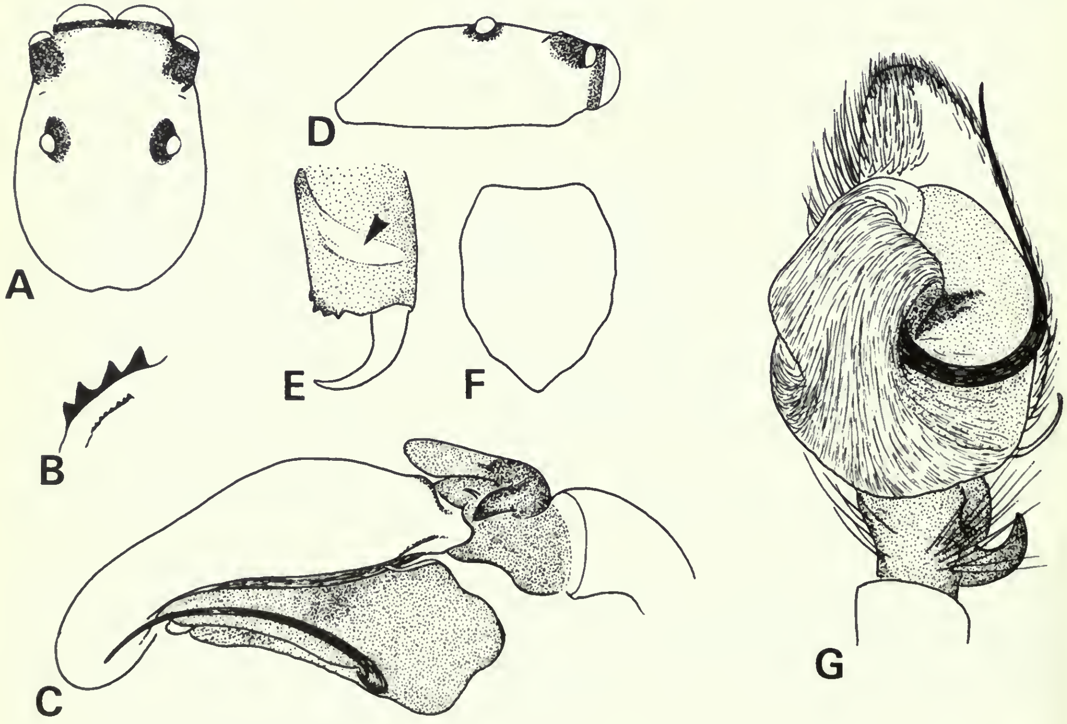

Fig. 6 *Hispo frenata* (Simon), lectotype ♂: A, carapace, dorsal view; B, cheliceral teeth; C, palp, lateral view; D, carapace, lateral view; E, chelicera, showing furrow; F, sternum; G, palp, ventral view.

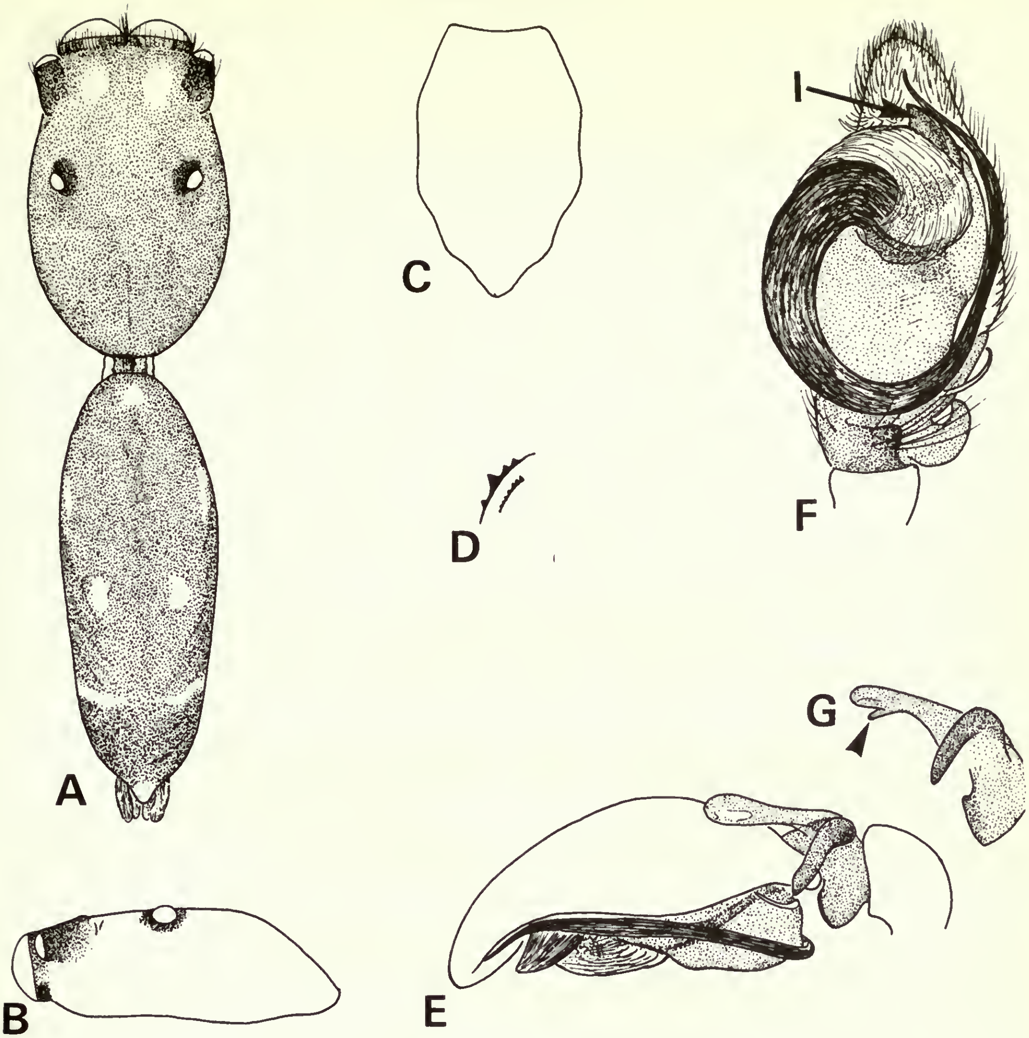

Fig. 7 *Hispo tenuis* sp. n., holotype ♂: A, dorsal view; B, carapace, lateral view; C, sternum; D, cheliceral teeth; E, palp, lateral view; F, palp, ventral view; G, tibial apophysis, lateral aspect, viewed slightly from below.

other leg spines few and moderately weak. *Palp* (Fig. 6C, G): additional spurs on the tibial apophyses are lacking in this species.

Dimensions (mm): total length 4·32; carapace length 2·04, breadth 1·52, height 0·84; abdomen length 2·2; eyes, anterior row 1·36, middle row 1·08, posterior row 1·10; quadrangle length 1·0. *Ratios*: AM : AL : PM : PL :: 12 : 5·5 : 1 : 4, AL–PM–PL :: 5·5–11.

DISTRIBUTION. Madagascar.

MATERIAL EXAMINED. Madagascar: Imerina, Lectotype ♂ (*Camboué*) (MNHN, Paris. 13127).

Hispo tenuis sp. n.
(Fig. 7A–F)

DIAGNOSIS. *Hispo tenuis* is closely related to *H. frenata* (Simon), *H. sulcata* sp. n., and *H.*

macfarlanei sp. n., but may be distinguished by the more robust embolus (Fig. 7F) and presence of a prolateral spur on the dorsal prong of the tibial apophysis (Fig. 7G).

FEMALE. Unknown.

MALE HOLOTYPE. *Carapace* (Fig. 7A, B): finely rugose to finely punctate-reticulate within eye region; brownish orange, weakly iridescent. *Eyes*: with black surrounds; anteriors contiguous, apices slightly procurved, fringed in whitish hairs. *Clypeus*: with scattered long pale brown hairs. *Chelicerae*: finely rugose; dark brown, weakly iridescent; promargin with 4 teeth, retromargin with 6 or 7 forming a serrated ridge. *Maxillae and labium*: brownish orange, inner distal margin of maxillae whitish. *Sternum* (Fig. 7C): brownish orange lightly tinged black. *Abdomen*: mottled yellow-brown and black with whitish markings; anal tubercle whitish. *Legs*: legs I longest, brownish orange to light brown; other legs yellow-brown to whitish yellow with blackish femora. Spination of legs I: metatarsi with 1 prolateral spine; other leg spines few and weak. *Palp* (Fig. 7E–G): embolus robust, prolateral spur on tibial apophysis can only be seen when palp is viewed slightly from below (Fig. 7G).

Dimensions (mm): total length 4·08; carapace length 1·68, breadth 1·05, height 0·6; abdomen length 2·12; eyes, anterior row 0·96, middle row 0·78, posterior row 0·84; quadrangle length 0·8. *Ratios*: AM : AL : PM : PL :: 9 : 4 : 1 : 3·5, AL–PM–PL :: 5–9.

VARIATION. ♂ total length 3·6 to 4·08 mm, carapace length 1·48–1·68 mm (3 specimens).

DISTRIBUTION. Madagascar.

MATERIAL EXAMINED. Sri Lanka: Kandy, lectotype juvenile, *(E. Simon)* (MNHN Paris paratypes 2 ♂♂, x.1971 (*B. Ranson,* MT. 142.876) (MRAC, Tervuren).

Hispo sulcata sp. n.
(Fig. 8A–I)

DIAGNOSIS. *Hispo sulcata* is closely related to *H. frenata* (Simon), *H. tenuis* sp. n., and *H. macfarlanei* sp. n., but can be distinguished by the presence of a spur on the lateral prong of the tibial apophysis (Fig. 8B, C).

FEMALE. Unknown.

MALE HOLOTYPE. *Carapace* (Fig. 8H): finely rugose to aciculate in eye region; dark brown, quadrangle paler, shiny with a greenish iridescent tinge on thoracic part under some angles of illumination. *Eyes*: with black surrounds; anteriors more or less contiguous, apices level, sparsely fringed in whitish hairs. *Clypeus*: sparsely fringed in fine whitish hairs. *Chelicerae* (Fig. 8F, G): smooth with deep cross furrows; orange-brown, shiny; promargin with 5 teeth, retromargin with 6 or 7 forming a serrated ridge. *Maxillae* (Fig. 8E, H): blades more or less rounded, but with a broad groove laterally; orange-brown. *Labium*: orange-brown. *Sternum* (Fig. 8D): yellow-brown, shiny. *Abdomen*: as in *H. pullata,* but whitish markings less distinct. *Legs*: legs I longest, dark brownish orange; other legs yellow-brown to orange-brown. Spination of legs I: tibiae with 1 distal ventral spine, femora with 2 dorsal and 1 distal proventral; other spines weak, but more numerous especially on legs III–IV. *Palp* (Fig. 8A–C): the spur on the lateral prong of the tibial apophysis is best seen when viewed from slightly below.

Dimensions (mm): total length 4·9; carapace length 2·1, breadth 1·64, height 0·23; abdomen length 2·68; eyes, anterior row 1·4, middle row 1·12, posterior row 1·16; quadrangle length 1·04. *Ratios*: AM : AL : PM : PL :: 12 : 6 : 1 : 5, AL–PM–PL :: 6–12.

DISTRIBUTION. Madagascar.

MATERIAL EXAMINED. Madagascar: holotype ♂, no other data, (MCZ, Harvard).

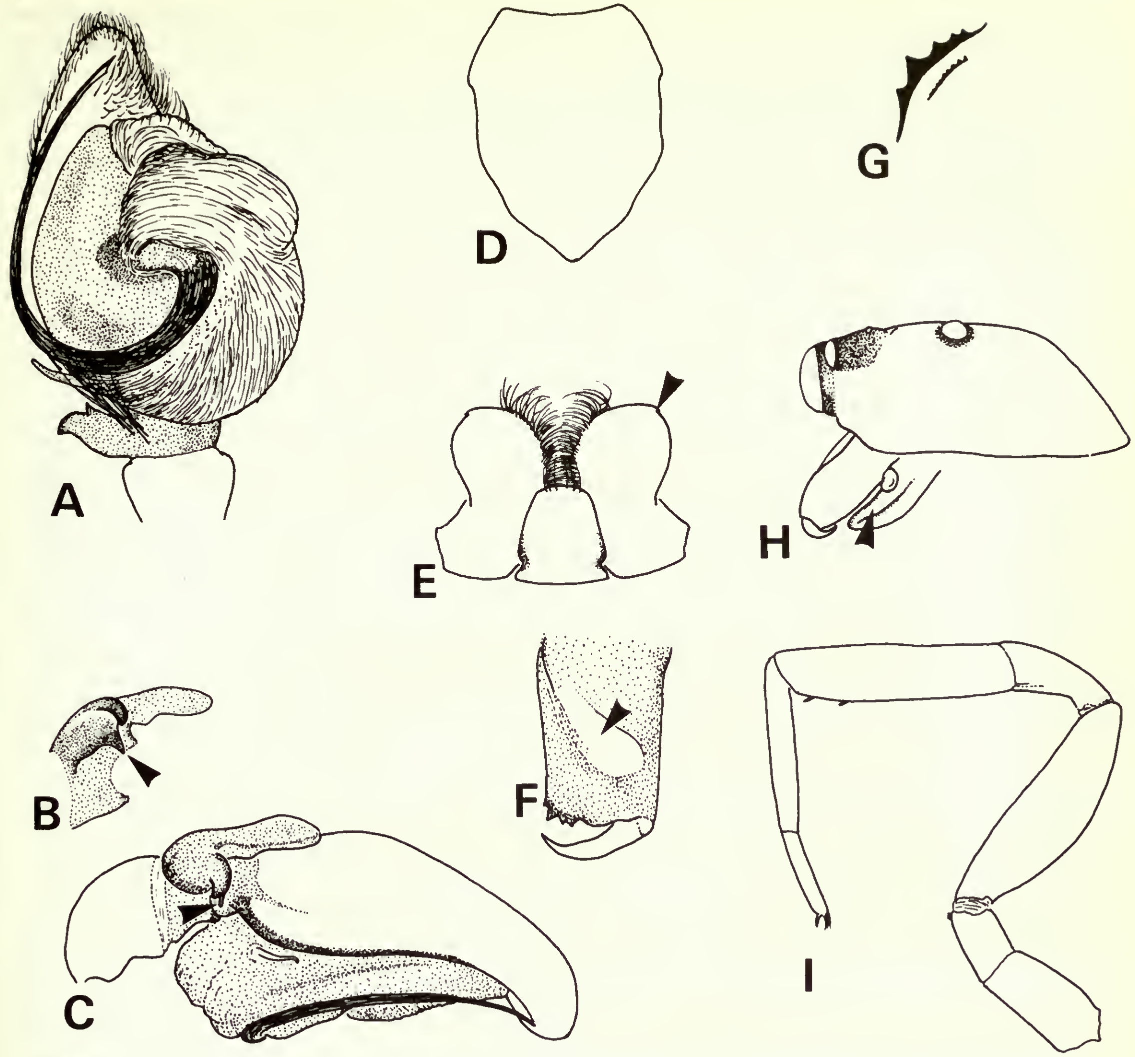

Fig. 8 *Hispo sulcata* sp. n., holotype ♂: A, palp, ventral view; B, tibial apophysis, lateral aspect, viewed from below; C, palp, lateral view; D, sternum; E, maxillae and labium; F, chelicera, showing furrow; G, cheliceral teeth; H, carapace, lateral view; I, leg I.

Hispo macfarlanei sp. n.

(Fig. 9A–M)

DIAGNOSIS. *Hispo macfarlanei* is closely related to *H. frenata* (Simon), *H. tenuis* sp. n., and *H. sulcata* sp. n., but may be distinguished by the backward pointed spur on the dorsal prong of the tibial apophysis (Fig. 9J, K) and the presence of a small epigynal scape (Fig. 9C). It is not known if the scape is diagnostic for females, as females of *frenata, tenuis* and *sulcata* are unknown.

MALE HOLOTYPE. *Carapace* (Fig. 9A, B): finely rugose, shiny in eye region; dark reddish brown with light orange guanin within quadrangle and yellow-brown patch behind posterior lateral eyes; below posterior eyes and on thoracic sides narrow stripes of short white hairs. *Eyes*: with black surrounds; anteriors contiguous, apices level, sparsely fringed in fine shiny hairs. *Clypeus*: thinly clothed in fine shiny hairs. *Chelicerae* (Fig. 9F, I): smooth with shallow cross furrows; dark reddish brown, shiny; promargin with 4 contiguous teeth, retromargin with 9 or 10 forming a serrated ridge. *Maxillae and labium*: orange-brown. *Sternum* (Fig. 9H): yellow with darker margins, shiny. *Abdomen*: pale yellow to yellow-brown with blackish markings and spots of short white hairs; anal tubercle sparsely fringed in white hairs. *Legs*: legs I elongate (Fig. 9D), orange-brown, thinly clothed in light orange hairs with white haired patches on femora and upper parts of trochanters and coxae; other legs light

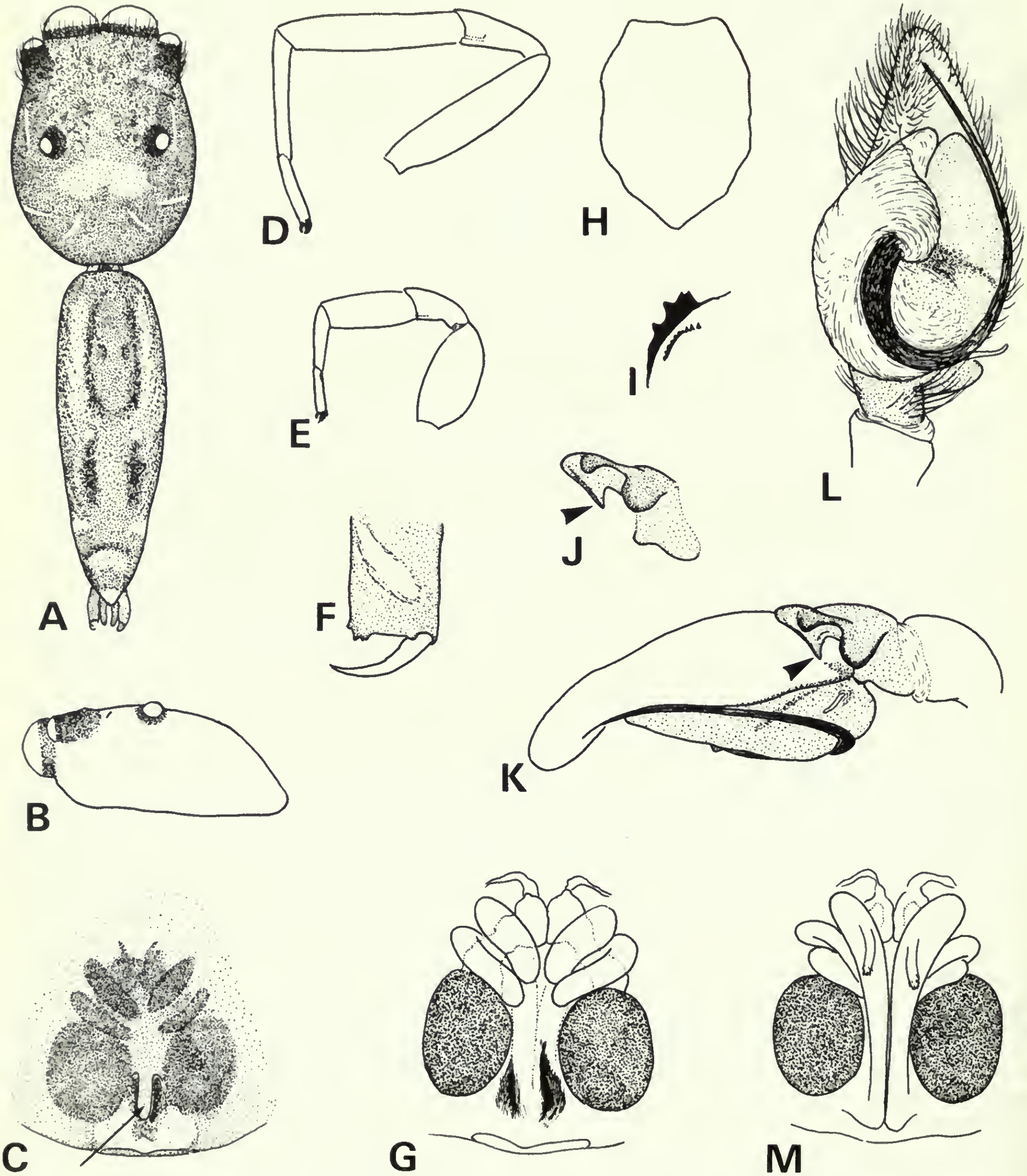

Fig. 9 *Hispo macfarlanei* sp. n., holotype ♂: A, dorsal view; B, carapace, lateral view; D, leg I; F, chelicera, showing furrow; H, sternum; I, cheliceral teeth; J, tibial apophysis, lateral aspect, viewed slightly from below; K, palp, lateral view; L, palp, ventral view. Paratype ♀: C, epigyne; E, leg I; G, vulva, ventral view; M. vulva, dorsal view.

orange-brown with yellowish trochanters and coxae, thinly clothed in fine pale yellowish hairs and with scattered white hairs on femora. Spination of legs I–II: femora with 3 dorsal spines; other leg spines moderately strong and numerous. *Palp* (Fig. 9J–L): tibial apophysis distinctive, unlikely to be confused with other known species of *Hispo*.

Dimensions (mm): total length 6·56; carapace length 2·84, breadth 2·16, height 1·24; abdomen length 3·68; eyes, anterior row 1·18, middle row 1·56 posterior row 1·58; quadrangle length 1·4. *Ratios*: AM : AL : PM : PL :: 17 : 7·5 : 1·4 : 6·5, AL–PM–PL :: 8–17.

FEMALE PARATYPE. Similar to ♂ except for the following. *Clypeus*: densely clothed in white hairs. *Chelicerae*: more bulbous anteriorly, furrow hardly apparent; dark orange, shiny; sparsely clothed in fine light brownish hairs. *Legs*: legs I (Fig. 9E) and II slightly more robust than in the ♂; legs I dark orange; other legs pale yellow-orange to dark orange. *Epigyne* (Fig. 9C, G, M): the small finger-like scape which arises from the anterior margin of the indistinct opening is surrounded by a dark red-brown substance, (?plugged) in the two epigynes available for study. Unfortunately it has not been possible to determine the precise nature of the scape, furthermore the spermathecae, which are blackish, may have altered during preservation.

Dimensions (mm): total length 7·92; carapace length 2·84, breadth 2·08, height 1·24; abdomen length 4·6; eyes, anterior row 1·87, middle row 1·48, posterior row 1·52; quadrangle length 1·4. *Ratios*: AM : AL : PM : PL :: 17 : 7·5 : 1·3 : 7, AL–PM–PL :: 8–16.

VARIATION. ♂ total length 4·88 to 6·84 mm, carapace length 2·44–2·84 mm (8 specimens). A second ♀ measures 6·36 mm total length, 2·72 mm carapace length.

DISTRIBUTION. Madagascar.

MATERIAL EXAMINED. Madagascar: Antongil, holotype ♂, paratypes 7 ♂♂, 2 ♀♀, *(A. Mocqueries)* (MNHN, Paris, 19541).

ETYMOLOGY. This species is named after Mr D. Macfarlane of the Commonwealth Institute of Entomology, London.

Hispo cingulata Simon
(Figs 10A–F; 11A–D)

Hispo cingulata Simon, 1886 : 394, ♀. LECTOTYPE ♀ (here designated) Madagascar, (MNHN, Paris, 5.487) [Examined]. Simon, 1901 : 450–452. Petrunkevitch, 1928 : 186. Bonnet, 1957 : 2220. Prószyński, 1971 : 417.

H. cingulatus: Roewer, 1954 : 985 [unjustified emendation].

DIAGNOSIS. *Hispo cingulata* is a distinctive species readily separated from other known species of *Hispo* by the presence of a 'conductor' (c) at the base of the embolus (Fig. 11A, B), and the structure of the epigyne (Figs 10F, 11C, D).

MALE FROM ANTONGIL. *Carapace*: finely rugose within eye region especially in depressions behind anterior median eyes; dark reddish, weakly iridescent; below posterior lateral eyes a narrow white haired stripe. *Eyes*: with black surrounds; anteriors contiguous, apices level, sparsely fringed in fine brown hairs. *Clypeus*: white hiared. *Chelicerae*: irregularly strigose with shallow vertical furrows; dark reddish, weakly iridescent; promargin with 4 contiguous teeth, retromargin with 8–10 forming a serrated ridge. *Maxillae and labium*: orange-brown. *Sternum*: elongate scutiform; orange-brown, shiny; slightly depressed opposite coxae I. *Abdomen*: yellow-brown tinged black with transverse bands of short white hairs; anal tubercle white haired. *Legs*: legs I–II robust, dark orange-brown clothed in stiff fine brownish hairs; other legs orange-brown lightly tinged black, slightly less hirsute. Spination of legs I–II: metatarsi with 1 proventral spine, tibiae with 2 ventral spines and 1 prolateral, femora with 3 dorsals and 2 prolaterals; other leg spines more numerous. *Palp* (Fig. 11A, B): the conductor (c) appears to be diagnostic for this species.

Dimensions (mm): total length 7·52; carapace length 2·4, breadth 2·2, height 1·2; abdomen

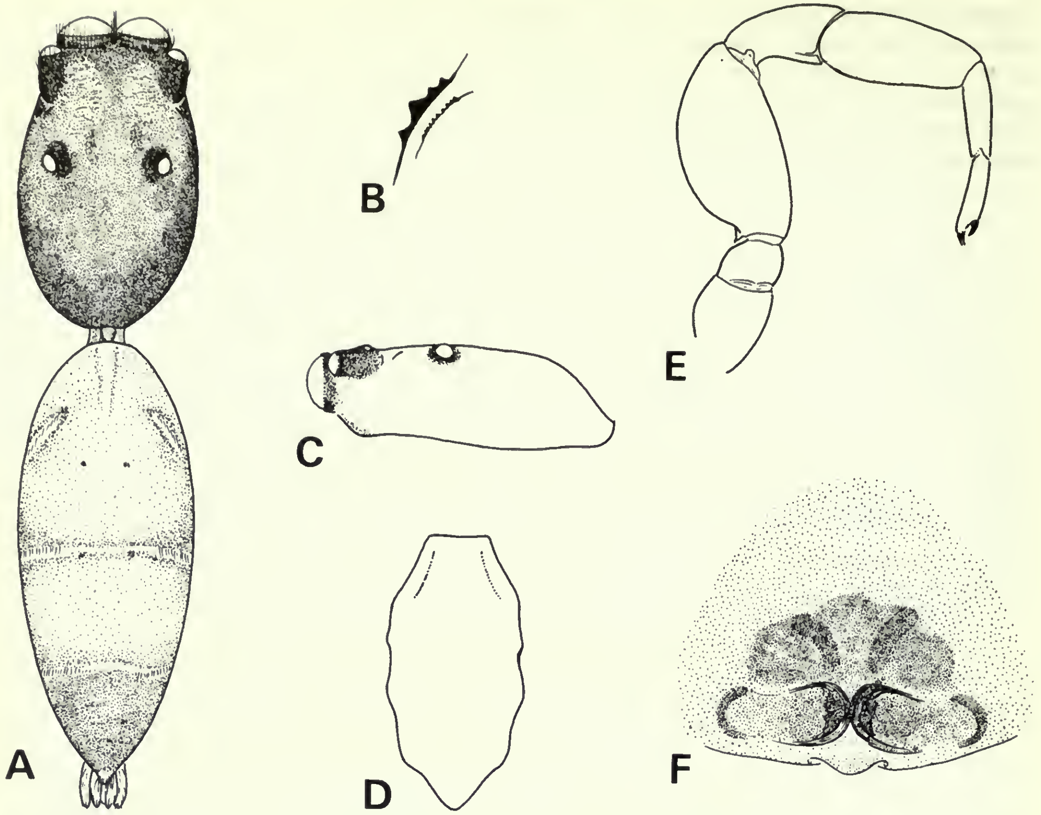

Fig. 10 *Hispo cingulata* Simon, lectotype ♀: A, dorsal view; B, cheliceral teeth; C, carapace, lateral view; D, sternum; E, leg I; f, eipgyne.

length 4·0; eyes, anterior row 1·84, middle row 1·44, posterior row 1·56; quadrangle length 1·52. *Ratios*: AM : AL : PM : PL :: 17 : 7·5 : 2 : 7, AL–PM–PL :: 8–18.

FEMALE LECTOTYPE (Fig. 10A–F): similar to ♂ except for the following. *Chelicerae* (Fig. 10B): slightly more bulbous anteriorly, furrow not apparent, irregularly strigose; dark reddish, shiny. *Epigyne* (Fig. 10F): vulva of another specimen (Fig. 11C, D).

Dimensions (mm): total length 8·5; carapace length 3·32, breadth 2·02, height 1·16; abdomen length 4·8; eyes, anterior row 1·7, middle row 1·36, posterior row 1·46; quadrangle length 1·46. *Ratios*: AM : AL : PM : PL :: 16 : 7 : 1·5 : 5·5, AL–PM–PL :: 8–18.

VARIATION. ♂ total length 5·84 to 7·52 mm, carapace length 2·4–3·36 mm (4 specimens). A ♀ in poor condition measures about 5·8 mm total length, 3·08 mm carapace length. The vertical cheliceral furrow is less evident in the smaller male and it is probably an allometric growth character.

DISTRIBUTION. Madagascar.

MATERIAL EXAMINED. Madagascar: lectotype ♀, (MNHN, Paris. 5.487); Antongil, 2 ♂♂, *(A. Mocqueries)* (MNHN, Paris. 19541); Ste Marie Island, 2 ♂♂, 1 ♀, *(A. Mocqueries)* (MNHN, Paris. 19944).

The ***bipartita***-group

This group is comprised of two species characterized by the presence of a fovea. *H. bipartita* Simon, is only known from the female, while *H. alboguttata* Simon is known from one subadult specimen.

Hispo bipartita Simon
(Fig. 12A–F)

Hispo bipartita Simon, 1903*a* : 1050. LECTOTYPE juvenile, (here designated) Sri Lanka (MNHN, Paris, 20406) [Examined]. Bonnet, 1957 : 2219 [*nomen nudum*]. Prószyński, 1971 : 417.

REMARKS. Bonnet, 1957 was mistaken in regarding the name *H. bipartita* as a *nomen nudum.* Simon (1903a) provided the briefest diagnosis and the name is therefore available. Furthermore an adult female in the collections of the British Museum (Natural History) is considered to be conspecific with the lectotype, a juvenile specimen.

DIAGNOSIS. *H. bipartita* seems to be closely related to *H. alboguttata* Simon, which is only known from a single subadult female. They are separated by their colour markings (Figs 12A, 13A), although this may or may not hold good for adults.

MALE. Unknown.

FEMALE FROM INDIA. *Carapace* (Fig. 12A, D): finely rugose in eye region to very finely papillate on thoracic part; orange-brown, sparsely clothed in short white lanceolate hairs. *Eyes*: with black surrounds; anteriors contiguous, apices slightly procurved, fringed in pale brown hairs with tufts outside the anterior lateral eyes. *Clypeus*: sparsely fringed in long whitish hairs. *Chelicerae* (Fig. 12C): irregularly strigose; lateral condyle prominent; orange-brown, weakly iridescent; promargin with 4 contiguous teeth, retromargin with 5 or 6 forming a serrated ridge. *Maxillae and labium*: pale orange to light yellow. *Sternum* (Fig. 12B): pale orange with darker margins. *Abdomen*: mottled yellow-brown and black with oblique fringes of short white hairs. *Legs*: legs I (Fig. 12E) and II enlarged; legs I pale orange, thinly clothed in pale orange hairs that arise from small circular pits (best seen on the tibiae); other legs yellow-brown to pale yellow. Spination of legs I: femora with 3 dorsal, almost hair-like spines; other leg spines few and weak. *Epigyne* (Fig. 12F): vulva not examined.

Dimensions (mm): total length 5·6; carapace length 2·4, breadth 1·64, height 0·56; abdomen length 3·12; eyes, anterior row 1·2, middle row 0·96, posterior row 1·2; quadrangle length 1·0. *Ratios*: AM : AL : PM : PL :: 10·5 : 5 : 2 : 5, AL–PM–PL :: 4–13.

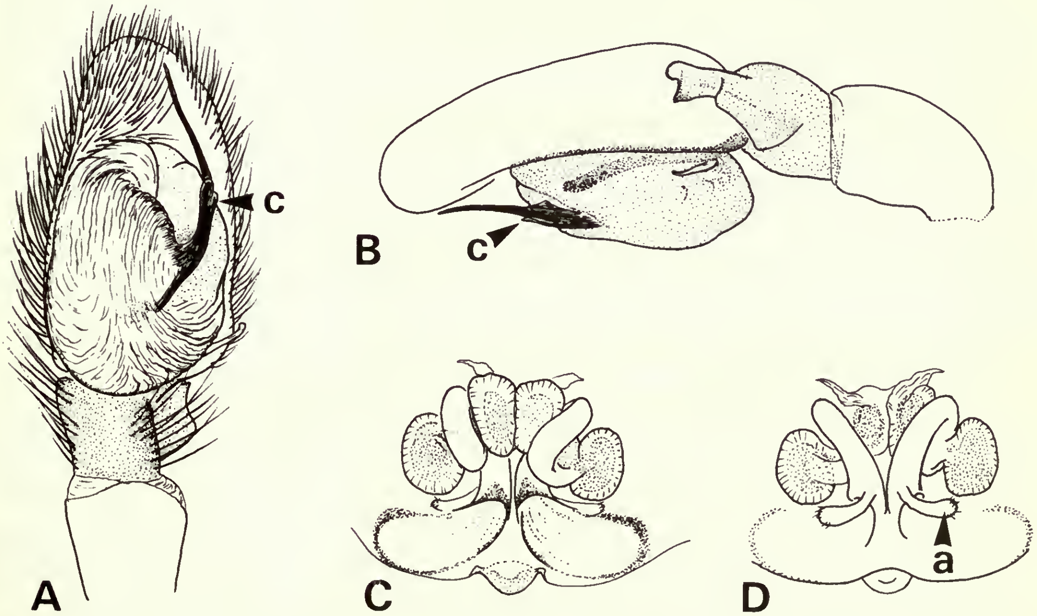

Fig. 11 *Hispo cingulata* Simon, ♂: A, palp, ventral view; B, palp, lateral view. ♀: vulva, ventral view; D, vulva, dorsal view.

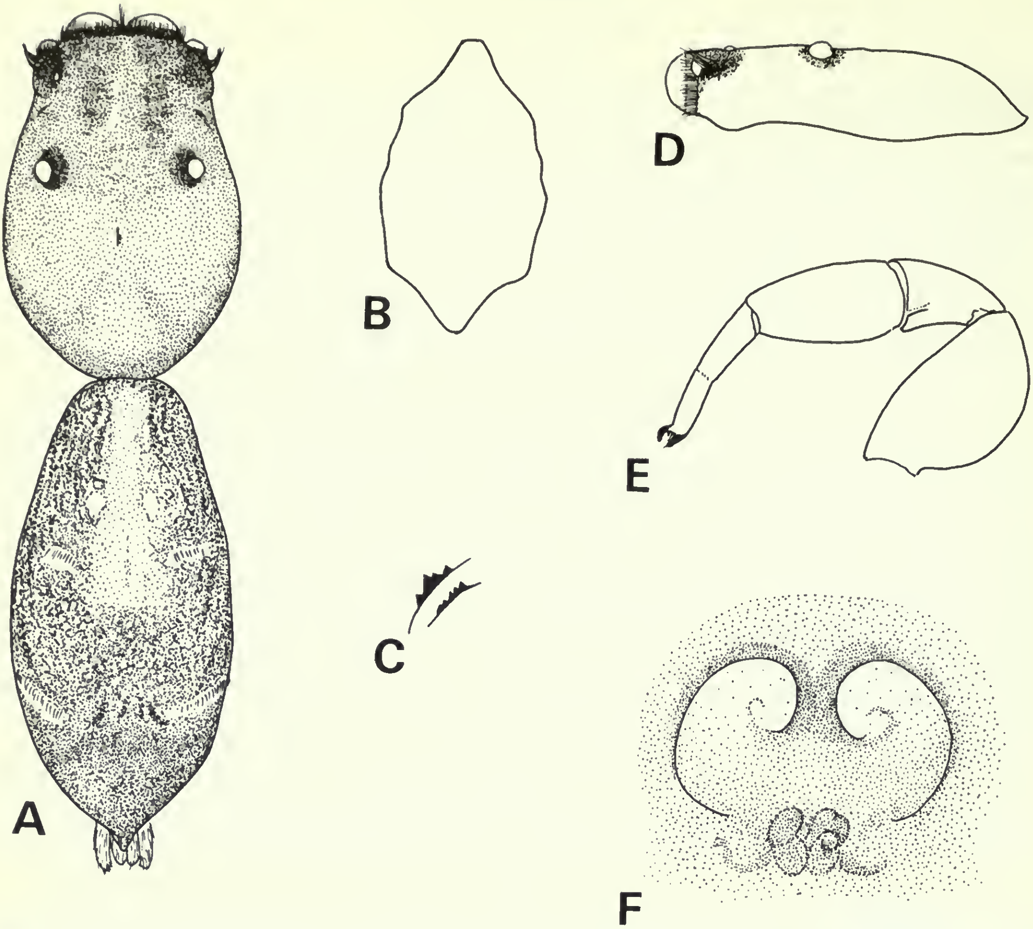

Fig. 12 *Hispo bipartita* Simon, ♀: A, dorsal view; B, sternum; C, cheliceral teeth; D, carapace, lateral view; E, leg I; F, epigyne.

Variation. The juvenile has the markings of the adult with a tuft of hairs outside of the anterior lateral eyes; the fovea, although present, is very small.

Distribution. India, Sri Lanka.

Material examined. Sri Lanka: Kandy, lectotype juvenile, *(E. Simon)* (MNHN, Paris, 20406). India: Madras, 1 ♀, (*N. S. Jambunathan*) (BMNH. 1923.12.21.76).

Hispo alboguttata Simon
(Fig. 13A–B)

Hispo alboguttata Simon, [June] 1903*a* : 1050. LECTOTYPE subadult ♀ (here designated) Sumatra (MNHN, Paris. 22180) [Examined]. Simon, [September] 1903*b* : 306. Roewer, 1954 : 985. Bonnet, 1957 : 2219. Prószyński, 1971 : 417.

Remarks. Although this species is only known from a subadult female the colour markings would appear to be distinctive and adults should be recognizable. The specimen is therefore figured and briefly described below.

Diagnosis. *H. alboguttata* can be distinguished from *H. bipartita* by the discoidal colour markings (Fig. 13A).

MALE. Unknown.

FEMALE LECTOTYPE (subadult). *Carapace* (Fig. 13A, B): orange with black markings in eye region; very sparsely clothed in fine orange and whitish hairs. *Eyes*: with black surrounds, anteriors contiguous, apices slightly procurved, fringed in whitish hairs with light orange hair tufts outside anterior lateral eyes. *Clypeus*: sparsely fringed in long whitish hairs. *Chelicerae*: pale yellow. *Maxillae, labium & sternum*: pale yellow, shiny. *Abdomen*: yellow-brown with pattern of discoidal white hair tufts and black markings; spinnerets yellow-brown, tinged black and thinly clothed in golden hairs. *Legs*: legs I–II enlarged; pale yellow, but legs I tinged black. Spines few and weak.

Dimensions (mm): total length 7·05; carapace length 3·04.

DISTRIBUTION. Sumatra.

MATERIAL EXAMINED. Sumatra: Palembang, Fôret du Nirou, lectotype subadult ♀, *(M. J. Bouchard)* (MNHN, Paris. 22180).

Species Incertae Sedis

Astaenorchestes continentalis Caporiacco

Astaenorchestes continentalis Caporiacco, 1949 : 462, ♀ juv. Kenya, Nairobi, 1944. Roewer, 1954 : 985.

This species was originally described from a juvenile female. I have been unable to examine the type and the species cannot be positively identified from the original description. However, the description is consistent with *Hispo* and the specimen was probably a juvenile of *H. inermis* which Caporiacco himself first described from Kenya.

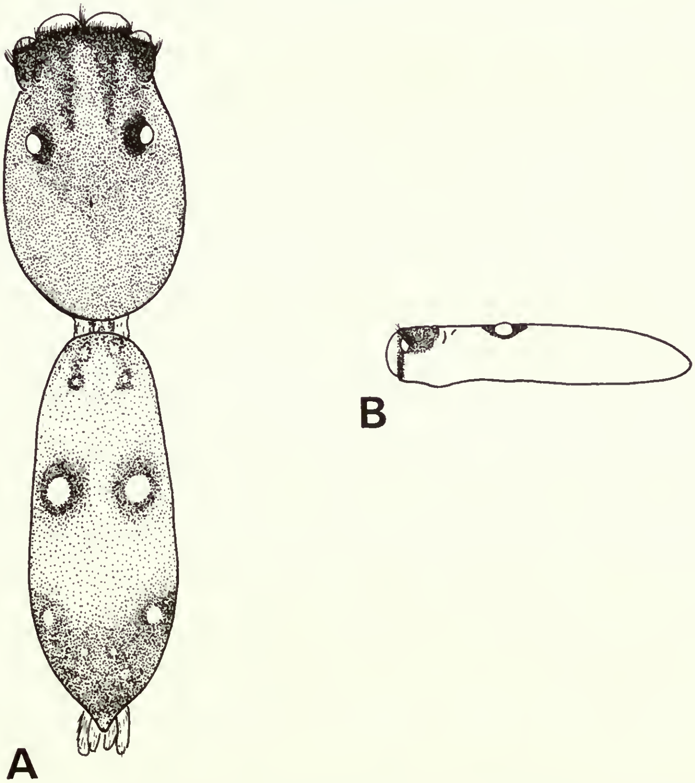

Fig. 13 *Hispo alboguttata* Simon, lectotype, subadult ♀: A, dorsal view; B, carapace, lateral view.

Acknowledgements

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A revision of the spider genus *Phaeacius* (Araneae : Salticidae)

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Introduction

Phaeacius Simon 1900 is a small genus of oriental salticids comprised of five known species three of which are described here as new. They are characterized by the presence of a long slender secondary conductor in males (Fig. 5C) and a specialized patch of spatulate setae, of unknown function, on the underside of coxae IV in females. It is unfortunate that the biology is unknown as it would be of interest to compare the behaviour of these salticids with that of *Portia* Karsch, a closely related genus of detritus mimics, some species of which build webs of their own as an aid to capture prey or invade the webs of other spiders and feed on the occupants (Wanless, 1978*b*). In spite of their large size (total length 7·5 to 11·5 mm) *Phaeacius* species are rare in museum collections and in the majority of cases only the types were available for study.

The measurements were made in the manner described by Wanless (1978*a*), but for the leg spination the system adopted is that used by Platnick and Shadab (1975).

Genus ***PHAEACIUS*** Simon

Phaeacius Simon, 1900 : 32. Type species *Phaeacius fimbriatus* Simon, by original designation. Simon, 1901 : 406–408. Waterhouse, 1902 : 280. Petrunkevitch, 1928 : 182. Roewer, 1954 : 935. Bonnet, 1958 : 3493.

Cocalus: Thorell, 1892 : 353 [in part].

DEFINITION. Medium to large spiders ranging from about 7·5 to 11·5 mm in length. Sexual dimorphism not marked. Most species hirsute, with similar colour patterns consisting of white marginal carapace bands and leaf-like abdominal markings composed of setae which are easily rubbed; abdominal markings may also include granules of subcutaneous guanin (Fig. 9A) possibly an artifact of preservation. *Carapace*: of medium height, longer than broad, widest between coxae II–III, lateral margins with distinct membraneous border (arrowed in Fig. 5E); fovea long and sulciform, situated just behind posterior median eyes; eye region finely punctate and weakly iridescent (evident only in rubbed specimens). *Eyes*: set on well developed tubercles, with black surrounds that are normally covered in hairs; arranged in three transverse rows comprised of anterior medians and anterior laterals, posterior medians, and posterior laterals; anteriors densely fringed in hairs, more or less subcontiguous with apices slightly procurved in frontal view; anterior medians largest, anterior laterals more than half diameter of anterior medians; posterior medians relatively large, positioned slightly closer and on or slightly inside optical axis of anterior laterals, posterior laterals almost as large as anterior laterals, set slightly closer together and well inside lateral margins of carapace; quadrangle formed by posterior median and posterior lateral eyes broader than long and widest posteriorly; entire quadrangle (measured from base of anterior medians to posterior margin of posterior laterals) occupying between 37 and 44 per cent of carapace length. *Clypeus*: between 25 and 36 per cent of diameter of anterior median eyes; clothed in hairs; ventrally a sometimes rather broad segmental membrane bearing a median subtriangular sclerite. *Chelicerae*: robust; more or less parallel, slightly inclined anteriorly; basal region usually clothed in hairs, short in central area, long on lateral

Bull. Br. Mus. nat. Hist. (Zool.) **41**(4): 199–212 Issued 26 November 1981

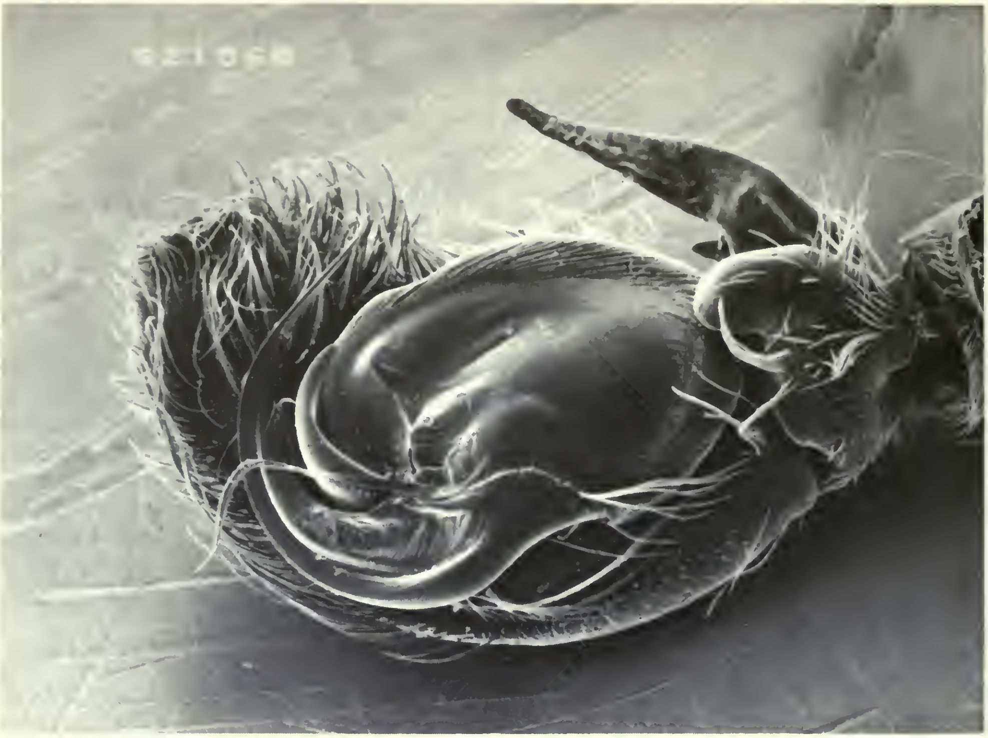

Fig. 1 *Phaeacius lancearius* (Thorell), ♂ palp, × 32. Note distorted secondary conductor.

margins; promargin with three teeth, retromargin with three to five. *Maxillae*: moderately long, subparallel. *Labium*: tongue-shaped, moderately long, slightly greater than half maxillae length. *Sternum*: elongate scutiform; margins not deeply excavated. *Coxae*: subequally robust or coxae IV slightly larger; in females coxae IV with spatulate setae on ventral surface. *Pedicel*: short. *Abdomen*: elongate ovoid with two pairs of impressed spots, the anterior pair the least conspicuous; spinnerets moderately long, posteriors longest with apical conical segment bearing moderately elongate spiggots, anteriors robust, medians and posteriors relatively slender; tracheal system not examined (insufficient material), spiricle an indistinct transverse slit near base of anterior spinnerets; former position of colulus indicated by hair tuft; anal tubercle a well developed pointed cone. *Legs*: moderately long and robust; spines strong and numerous; ornate fringes lacking, but female tarsi I–II and metatarsi I–II with fine ventral setae; claws pectinate scopulae lacking. *Female palps*: moderately long and robust with terminal claw. *Male palps*: large, usually dark; moderately complex and morphologically similar; densely clothed in hairs (not shown in figures). Tibiae with massive retrolateral apophysis, ventral apophysis and sometimes an intermediate apophysis; cymbium with small basal protuberance and characteristic profile in dorsal view (Figs 4E; 8B); embolus (e) robust, long and curved with conspicuous pars pendula (p); primary conductor lacking; secondary conductor (sc) translucent long, slender and curved, arising from membraneous region which appears to separate the embolic base from the tegulum (Fig. 4A), also arising from the membraneous region, below the embolic base, a short apophysis (a) (Figs 2E; 6B); tegulum (t) with pronounced tegular furrow (tf), peripheral seminal ducts (sd) and retrolateral striae (s) (Figs 1; 2A–F). *Epigynes*: large and dark; orifice paired, ovoid to furrowed, opening of looped introductory ducts lying alongside inner margins. Internal structure not examined (insufficient material).

The secondary conductor clearly arises from a membraneous region of the tegulum which lies adjacent to the embolic base (Fig. 2C, D). This region seems to be homologous with a

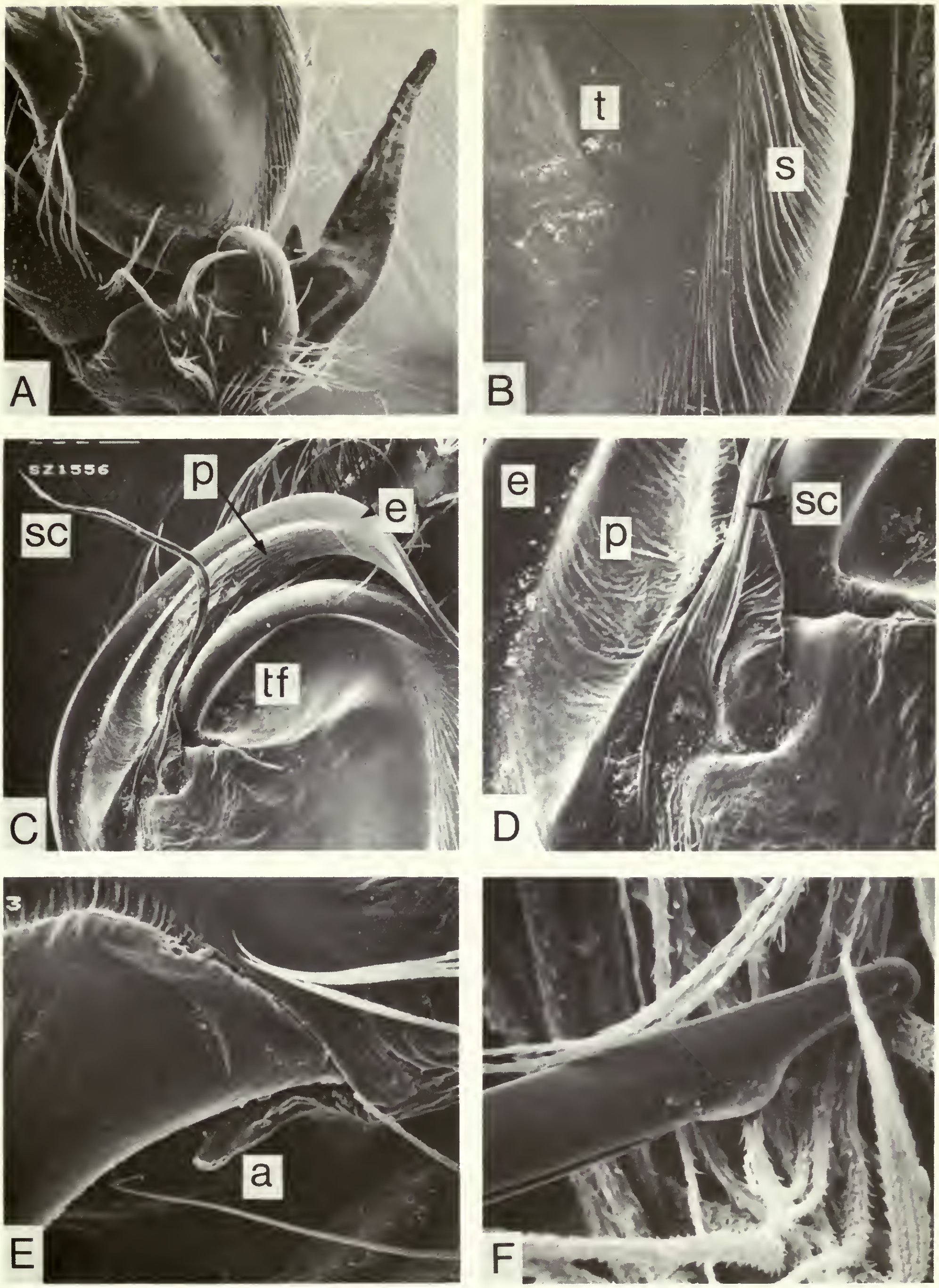

Fig. 2 *Phaeacius lancearius* (Thorell), ♂ palp: A, ventral and retrolateral tibial apophyses, × 32; B, tegulum with striae, × 80; C, embolus secondary conductor and tegular furrow, × 55; D, origin of secondary conductor, × 160; E, apophysis protruding from below embolic base, × 580; F, tip of embolus, × 700.

similar area found in some species of *Portia* and referred to as a tripartite membrane in Wanless (1978*b*). The dorsal and prolateral elements of the tripartite membrane are not evident in *Phaeacius.*

Affinities. *Phaeacius* seems on the basis of the elongate fovea, procurved anterior eye row and male palpal structure to be most closely related to the *schultzii*-group of species in the genus *Portia* Karsch (see Wanless, 1978*b*). The *kenti*-group of *Portia* would now appear to require a new genus. However, for the present I am reluctant to propose formal changes because morphological characters and relationships between other genera in the subfamily Boethinae are largely unknown.

List of species in the genus *Phaeacius* Simon, 1900

Phaeacius canalis sp. n.
P. fimbriatus Simon, 1900
P. lancearius (Thorell, 1895)
P. malayensis sp. n.
P. saxicola sp. n.

Remarks. Simon (1901) transferred *Cocalus ramipalpis* Thorell, from Sumatra, into *Phaeacius*, but to judge from his illustration (Fig. 435, g) the species probably belongs in *Boethus* and is therefore not included in the present revision.

Key to species of *Phaeacius*

Males (males of *saxicola* are unknown)

1 Dorsal prong of retrolateral tibial apophysis long (Fig. 8C) (Phillipines) . **canalis** sp. n. (p. 209)
– Dorsal prong of retrolateral tibial apophysis short (Figs 4C; 5F; 6A) 3
2 Intermediate tibial apophysis present (Fig. 6B) (Singapore) . . . . **malayensis** sp. n. (p. 205)
– Intermediate tibial apophysis lacking 3
3 Retrolateral tibial apophysis relatively short and broad, median notch moderately conspicuous (Figs 4C; 5B) (Java) . . . . **fimbriatus** Simon (p. 202)
– Retrolateral tibial apophysis relatively long and narrow, median notch inconspicuous (Fig. 5A, F) (Burma) . . . . **lancearius** (Thorell) (p. 205)

Females (females of *lancearius* are unknown)

1 Epigynal openings subovoid (Fig. 9C) (Nepal) . . . . **saxicola** sp. n. (p. 210)
– Epigynal openings relatively narrow or furrowed 2
2 Epigynal openings furrowed (Fig. 8G) (Phillipines) . . . . . . **canalis** sp. n. (p. 209)
– Epigynal openings relatively narrow (Figs 4D; 7C) 3
3 Anterior margin of epigynal orifice level with anterior loop of seminal duct (Fig. 7C) (Sumatra) . . . . **malayensis** sp. n. (p. 205)
– Anterior margin of epigynal orifice posterior to anterior loop of seminal duct (Fig. 4D) (Java) . . . . **fimbriatus** Simon (p. 202)

Phaeacius fimbriatus Simon
(Figs 4A–H; 5B)

Phaeacius fimbriatus Simon, 1900 : 32, ♀. lectotype ♀ (here designated) Java (MNHN, Paris) [examined]. Simon 1901 : 406–408. Reimoser, 1925 : 90. Petrunkevitch, 1928 : 182. Roewer, 1954 : 935. Bonnet, 1958 : 3493.

Diagnosis. *P. fimbriatus* seems to be most closely related to *P. lancearius*, but may be distinguished by the form of the retrolateral tibial apophysis (Figs 4A, C; 5B) which is shorter and somewhat broader basally. Also, the median notch (arrowed in Fig. 5B) is more

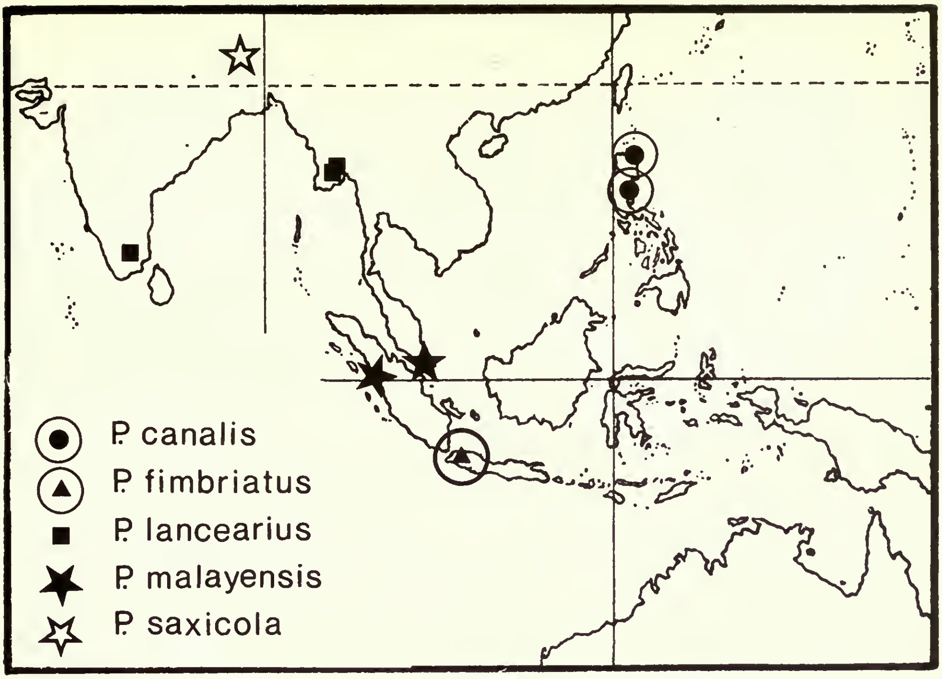

Fig. 3 Distribution of *Phaeacius* spp.

pronounced. In the lectotype the embolus is clearly shorter than that of *P. lancearius*, but the tip appears to have broken off. Unfortunately the right palp is missing and no other specimens are available for comparison.

REMARKS. A female labelled '20032 Phaeac. fimbriatus E.S. Java: Gedi (Fr)' corresponds with the data given in the original description, but was accompanied by an apparently conspecific male not mentioned by Simon. As no other specimens can be found in the Simon collection (MNHN, Paris) the single female is presumed to be the type specimen. The male is described below.

FEMALE LECTOTYPE. *Carapace* (Fig. 4B, G): orange-brown with sooty markings; eye region finely punctate and weakly iridescent under some angles of illumination; badly rubbed, but patches of recumbent short whitish hairs present. *Eyes*: with black surrounds; fringed in whitish hairs especially AM. *Clypeus*: clothed in brownish orange hairs. *Chelicerae*: orange, shiny; basal region clothed in whitish hairs; promargin with three teeth, retromargin with four. *Maxillae*: light orange grading to whitish yellow on inner distal margins. *Labium*: pale orange tipped whitish yellow. *Sternum*: pale yellow with light orange margins; clothed in light yellow hairs. *Coxae*: pale yellow to yellow-brown. *Abdomen*: with two pairs of impressed spots; light brownish grey with numerous granules of yellowish subcutaneous guanin and lateral dark brown markings forming a foliated pattern more or less as in *P. saxicola* sp. n. (Fig. 9A); basal region with rather scanty clumps of white and dark brown hairs, otherwise rubbed; spinnerets pale yellow-brown. *Legs*: yellow-brown with vague orange-brown markings; spines numerous and strong. Spination of legs I: metatarsi v 1–0–0, p 1–1–0, r 1–1–1; tibiae v 1–4–1, p 1–0–1, r 1–0–1, d 1–1–0; patellae p 1–0–0, r 1–0–0; femora p 0–1–1, d 0–2–3. *Epigyne* (Fig. 4D): dark reddish brown; clothed in light orange-brown hairs.

Dimensions (mm): total length 8·72; carapace length 3·88, breadth 3·16, height 1·76; abdomen length 4·64; eyes, anterior row 2·16, middle row 1·92, posterior row 2·02;

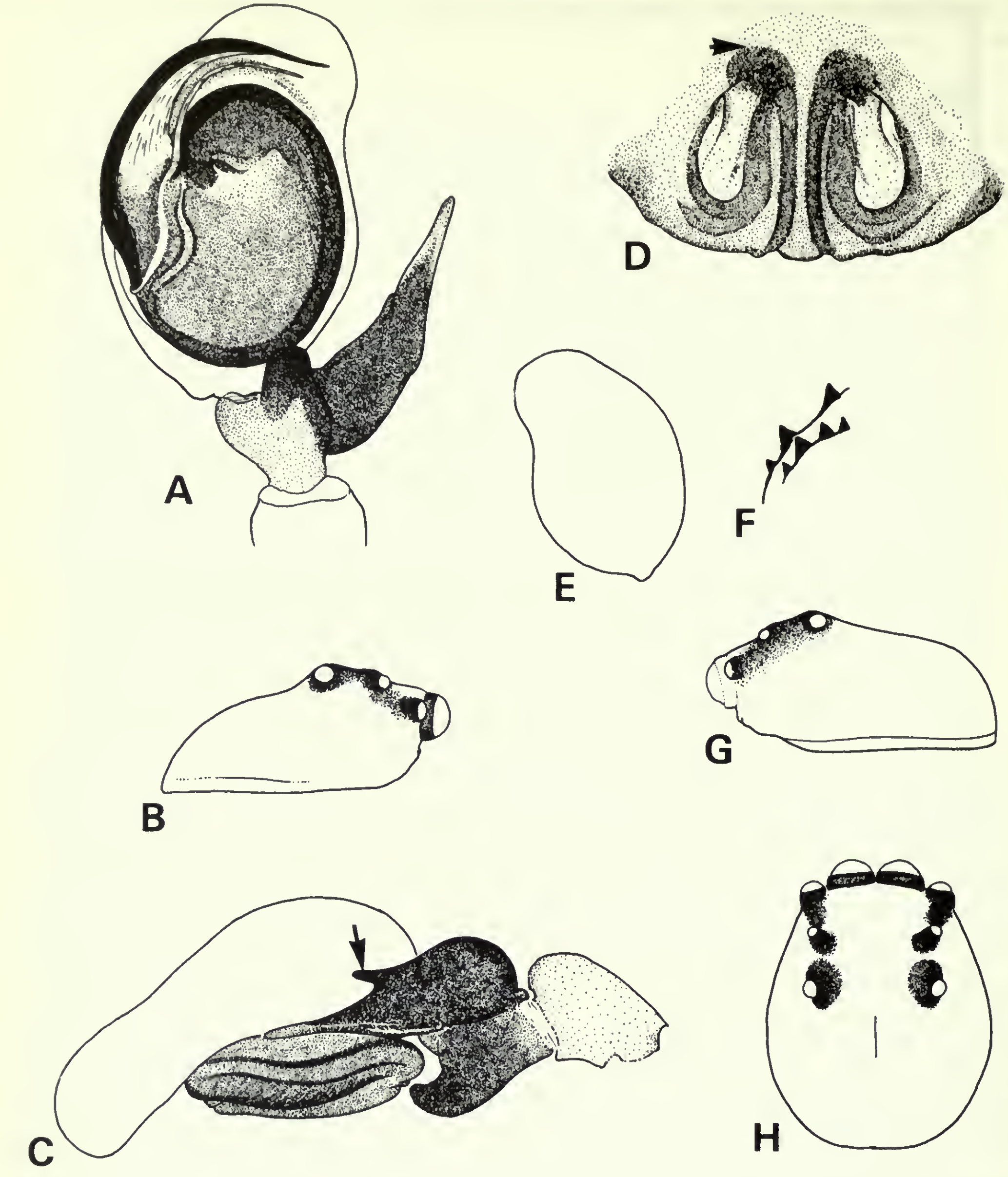

Fig. 4 *Phaeacius fimbriatus* Simon, ♂: A, palp, ventral view; C, palp, ectal view; E, palpal cymbium, dorsal view; G, carapace, lateral view. ♀ lectotype: B, carapace lateral view; D, epigyne; F, cheliceral teeth; H, carapace, dorsal view.

quadrangle length 1·6. *Ratios*: AM : AL : PM : PL : 16 : 9 : 6 : 8·4; AL–PM–PL : 11·5–14; AM : CL (clypeus) : 16 : 4.

MALE (formerly undescribed) FROM JAVA. Similar to ♀ except for the following: *Carapace* (Fig. 4G): with uneven marginal band of white hairs. *Chelicerae*: not quite as robust as in ♀; basal region densely clothed in white hairs noticeably long on lateral margins. *Abdomen*: more or less as in ♀, but guanin granules not evident. *Legs*: similar to ♀, but darker markings forming indistinct annuli on tibiae and metatarsi. Spination of legs I: metatarsi v 2–0–0, p

1–1–0, r 1–1–2, d 0–1–0; tibiae v 2–3–2, p 1–1–0, r 0–1–1, d 1–1–1; patellae p 1–0–0, r 1–0–0; femora p 0–1–1, d 0–2–1, r 0–0–1. *Palp* (Figs 4A, C; 5B): rather dark and thickly clothed in orange-brown hairs.

Dimensions (mm): total length 8·1; carapace length 3·8, breadth 3·24, height 2·0; abdomen length 4·32; eyes, anterior row 2·1, middle row 1·82, posterior row 1·96; quadrangle length 1·52. *Ratios*: AM : AL : PM : PL : 15 : 9 : 6 : 8; AL–PM–PL : 11–13; AM : CL : 15 : 5.

Distribution. Java.

Material examined. Java: Mons Gede, lectotype ♀, 1 ♂, (*Fruhstorfer*) (MNHN, Paris. 20032).

Phaeacius lancearius (Thorell)

(Figs 1; 2A–F; 5A, C–F)

Cocalus lancearius Thorell, 1895 : 357, ♂. LECTOTYPE ♂, (BMNH); PARALECTOTYPE ♂, (NR, Stockholm) (here designated), Burma [examined]. Bonnet, 1956 : 1173.

Phaeacius lancearius (Thorell): Roewer, 1954 : 935.

Diagnosis. *P. lancearius* seems to be most closely related to *P. fimbriatus,* but may be separated by the longer and somewhat narrower retrolateral tibial apophysis and the less pronounced median notch (arrowed in Fig. 5A). It is possible that intermediate forms may occur, but for the moment *P. lancearius* is regarded as a good species.

Female. Unknown.

Male lectotype. *Carapace* (Fig. 5D, E): greyish black with finely punctate orange-brown eye region; margins with broad uneven white haired bands, otherwise badly rubbed. *Eyes*: with black surrounds, irregularly fringed in whitish and light brown hairs (mostly rubbed). *Clypeus*: clothed in light brown hairs. *Chelicerae*: orange-brown, basal area clothed in whitish hairs, longest on outer lateral margins; promargin with three teeth, retromargin with four. *Maxillae*: dark brown grading to yellow-brown on inner distal margins. *Labium*: dark brown tipped yellowish brown. *Sternum*: yellow-brown with thin brownish margins, shiny; clothed in white hairs. *Coxae*: greyish, shiny. *Abdomen*: with two pairs of impressed spots; light greyish with granules of yellow guanin; sparsely and irregularly clothed in recumbent light brownish hairs; spinnerets greyish yellow. *Legs*: greyish brown to orange-brown; spines numerous and robust. Spination of legs I: metatarsi v 2–0–0, p 1–1–0, r 1–1–2, d 0–1–0; tibiae v 2–3–2, p 0–2–0, r 0–2–0, d 1–1–1; patellae p 1–0–0; femora p 0–1–1, d 0–1–4. *Palp* (Figs 1, 2A–F; 5A, C, F): very dark.

Dimensions (mm): total length about 7·76; carapace length about 3·7, breadth 3·08, height 1·6; abdomen length about 3·8; eyes, anterior row 1·95, middle row 1·68, posterior row 1·8; quadrangle length 1·48. *Ratios*: AM : AL : PM : PL : 14:9 : 5: 5:7; AL–PM–PL : 11–13; AM : CL : 14 : 5.

Variation. ♂ total length 7·76 to 8·72 mm, carapace length 3·72–4·0 mm (3 specimens). The paralectotype and the male from India are generally paler in colour, the carapace being orange to dark orange with a dense covering of mixed white and light orange hairs. The palps are also paler and densely clothed in light brownish hairs.

Distribution. Burma; India.

Material examined. **Burma:** Tharrawaddy, lectotype ♂, (*E. W. Oates*) (BMNH. 1895.9.21.1065); Tonghoo, paralectotype ♂, (E. W. Oates) (NR, Stockholm, 1607). **India:** Southern India, 1 ♂, no other data (BMNH).

Phaeacius malayensis sp. n.

(Figs 6A–E; 7A–C)

Diagnosis. *P. malayensis* is closely related to both *P. fimbriatus* and *P. lancearius*, but may

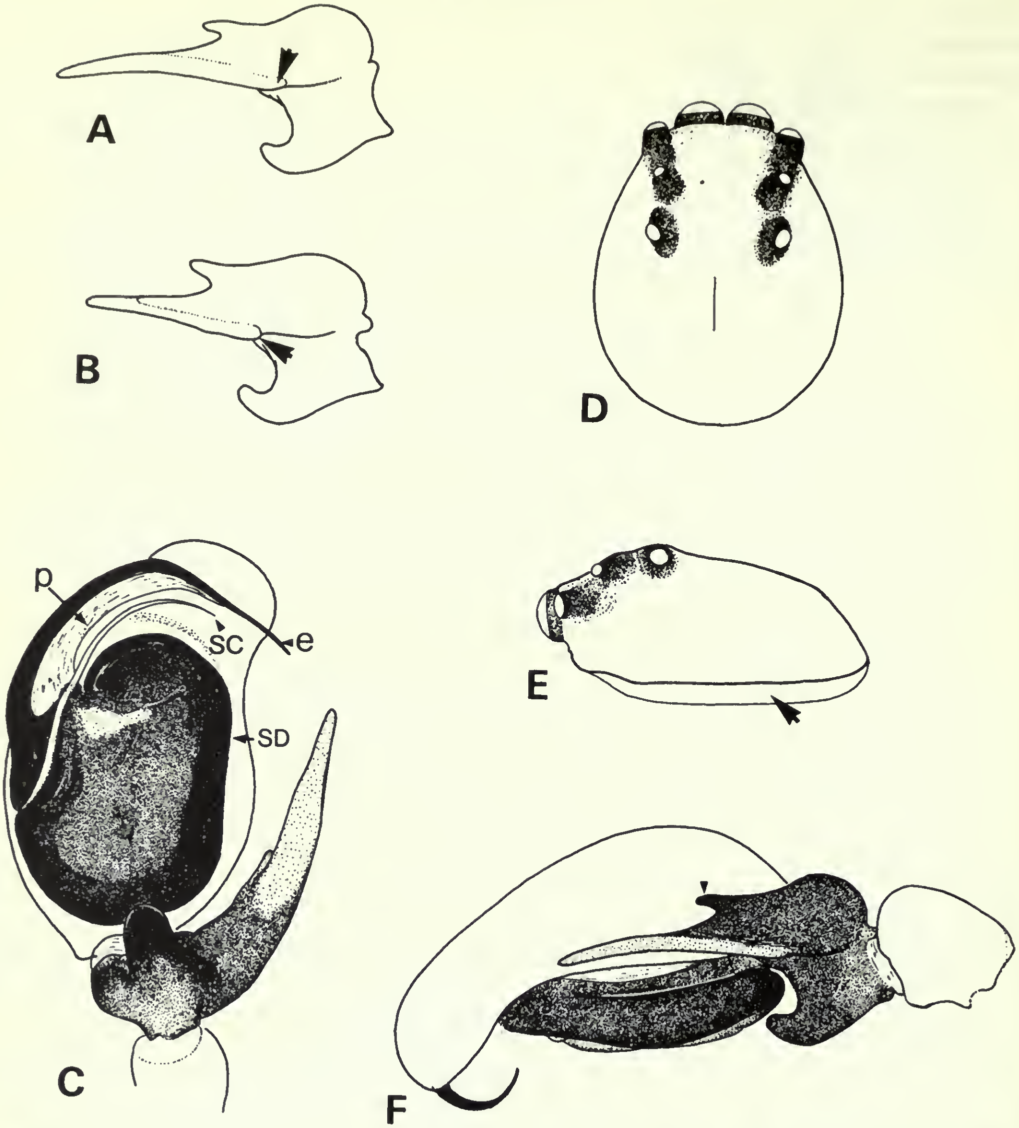

Fig. 5 (A, C–F) *Phaeacius lancearius* (Thorell) ♂ lectotype: A, palpal tibia, ectal view; C, palp, ventral view; D, carapace, dorsal view; E, carapace, lateral view; F, palp, ectal view. (B) *P. fimbriatus* Simon, ♂: palpal tibia, ectal view.

be distinguished by the presence of a pronounced apophysis lying between the ventral and retrolateral tibial apophyses (Fig. 6B) in males, and by having the anterior margin of the epigynal orifice more or less level with the anterior loop of the seminal duct (Fig. 7C) in females.

MALE HOLOTYPE. *Carapace* (Fig. 6D, E): light orange to orange-brown; finely punctuate with iridescent sheen in eye region; sparsely and irregularly clothed in recumbent white hairs (rubbed). *Eyes*: with black surrounds; irregularly clothed in whitish and pale golden hairs. *Clypeus*: fringed in light brown and whitish hairs. *Chelicerae*: pale orange; basal region white haired; promargin with three teeth, retromargin with four. *Maxillae*: light orange and mottled grey to whitish on inner distal margins. *Labium*: orange-brown tipped greyish white. *Sternum*: pale yellow with light orange margins, shiny; clothed in pale yellow hairs. *Coxae*: pale yellowish, shiny. *Abdomen*: rubbed; pale yellow with granules of whitish guanin and blackish lateral mottling (suggesting a foliated pattern as in other species of *Phaeacius*). *Legs*: yellowish orange; spines strong and numerous. Spination of legs I: metatarsi v 2–0–0, p 1–1–0, r 1–1–2, d 0–1–0; tibiae v 2–3–2, p 1–0–1, d 2–2–1; patellae p 1–0–0, r 1–0–0; femora p 0–1–1, d 0–2–2, r 0–0–1. *Palp* (Fig. 6A, B): densely clothed in light brown and whitish hairs which tend to obscure the apophyses that lies between the ventral and retrolateral apophyses.

Dimensions (mm): total length 8·0; carapace length 3·8, breadth 3·24, height 1·8; abdomen length 4·12; eyes, anterior row 2·16, middle row 1·92 posterior row 2·0; quadrangle length 1·68. *Ratios*: AM : AL : PM : PL : 16·5 : 9·5 : 6·5 : 9; AL–PM–PL : 11–13·5; AM : CL 16·5 : 6.

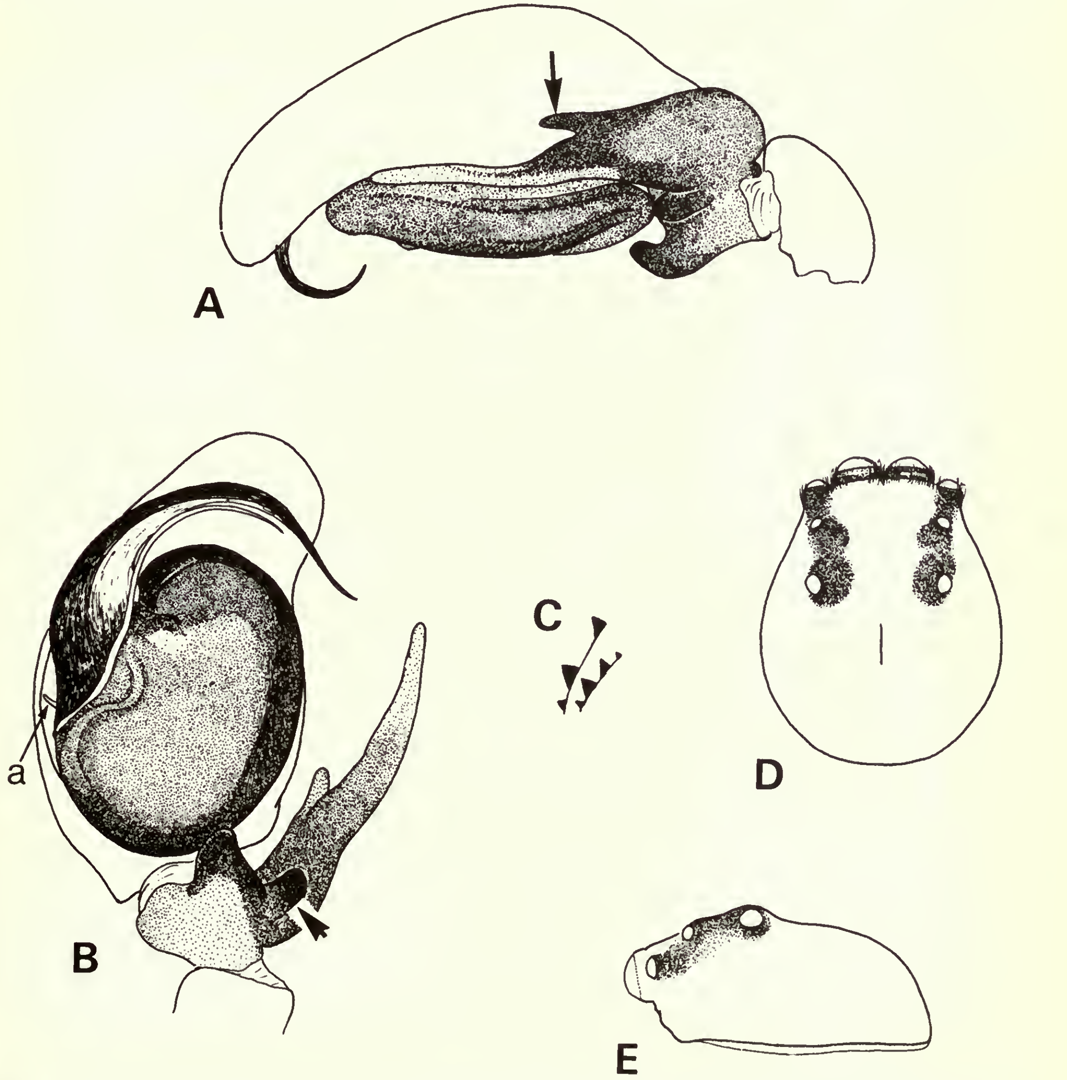

Fig. 6 *Phaeacius malayensis* sp. n., ♂ holotype: A, palp, ectal view; B, palp, ventral view; C, cheliceral teeth; D, carapace, dorsal view; E, carapace, lateral view.

FEMALE PARATYPE. *Carapace* (Fig. 7A): yellow-brown to light amber with sooty markings; clothed in short recumbent light brown and white hairs with narrow white haired marginal bands. *Eyes*: with black surrounds; densely fringed in white and pale amber hairs. *Clypeus*: fringed in long whitish hairs. *Chelicerae*: orange-brown; clothed in long white hairs; promargin with three teeth, retromargin with four. *Maxillae*: orange-brown with whitish inner distal margins. *Labium*: orange-brown tipped whitish. *Sternum* (Fig. 7B): pale yellow with dark margins, shiny; clothed in fine pale yellowish hairs. *Abdomen*: greyish yellow; sparsely clothed in light orange-brown hairs forming a leaf-like pattern with scanty tufts of long white hairs posteriorly. *Legs*: light yellow grading to yellow-brown distally with indistinct annuli on metatarsi; spines numerous and robust. Spination of legs I: metatarsi v 2–0–0, p 1–1–0, r 1–1–1; tibiae v 2–3–2, p 1–0–1, r 1–0–1, d 1–1–0; patellae p 0–1–0, r 0–1–0; femora p 0–1–1, d 0–1–4. *Epigyne* (Fig. 7C): large and dark, clothed in fine pale orange hairs.

Dimensions (mm): total length 8·96; carapace length 3·8, breadth 3·16, height 1·68; abdomen length 5·04; eyes, anterior row 2·12, middle row 1·8, posterior row 1·96; quadrangle length 1·6. *Ratios*: AM : AL : PM : PL : 15 : 9 : 6 : 9; AL–PM–PL : 12–14; AM : CL : 15 : 3.

DISTRIBUTION. Malaysia, Singapore; Sumatra.

MATERIAL EXAMINED. **Malaysia:** Singapore, holotype ♂, 1898 (*H. N. Ridley*) (BMNH, 1980.4.9.1). **Sumatra:** Lembang Anai, paratype ♀, xii.1974 (*W. S. Bristowe*) (BMNH. 1980.4.14.1).

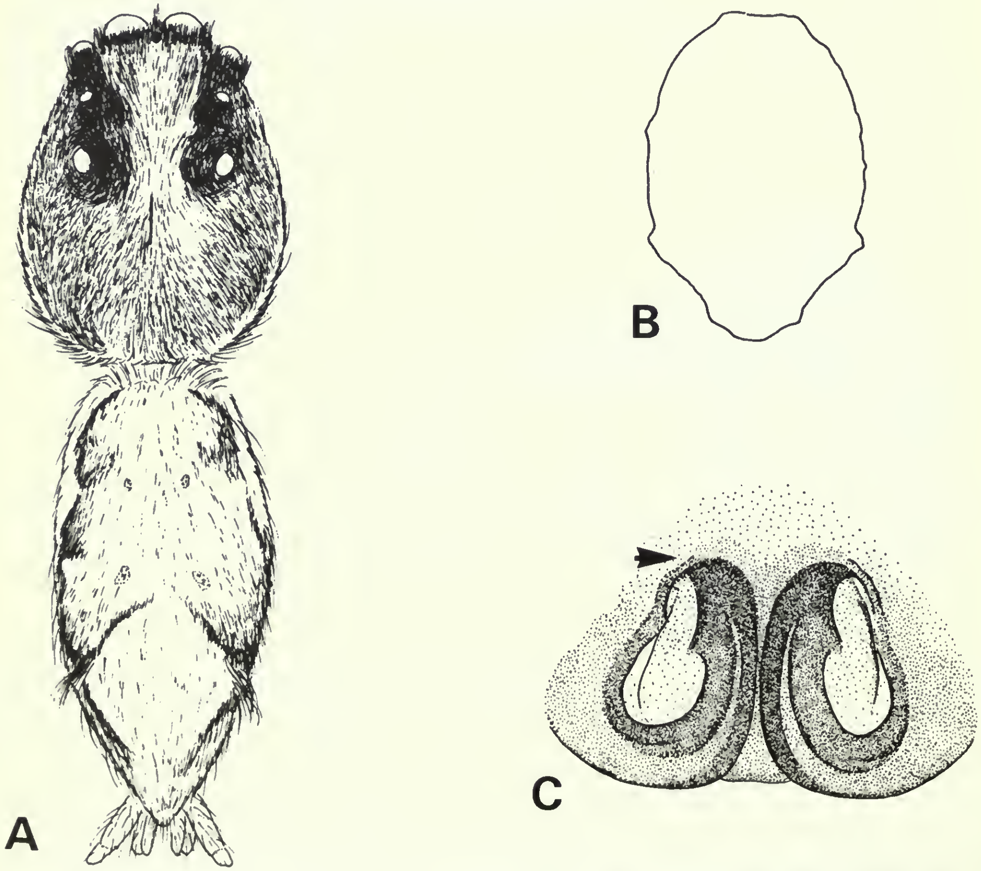

Fig. 7 *Phaeacius malayensis* sp. n., ♀ paratype: A, dorsal view; B, sternum; C, epigyne.

Phaeacius canalis sp. n.
(Fig. 6A–F)

DIAGNOSIS. *P. canalis* is a fairly distinctive species readily separated from other species of *Phaeacius* by the elongate dorsal prong of the retrolateral tibial apophysis (Fig. 6B) in males, and the grooved epigynal openings (Fig. 6F) in females.

HOLOTYPE MALE. *Carapace* (Fig. 6C, E): pale to dark amber with vague radiating markings; irregularly clothed in recumbent clear whitish and pale amber hairs (rubbed), from clypeus to posterior thoracic margin a wide uneven white haired band. *Eyes*: with blackish surrounds; densely fringed in whitish and pale amber hairs. *Clypeus*: clothed in pale amber hairs. *Chelicerae*: dark amber, shiny; basal half densely clothed in white hairs, longest on lateral margins; promargin with three teeth, retromargin with four. *Maxillae*: orange-brown grading to whitish yellow on inner distal margins. *Labium*: orange-brown tipped whitish

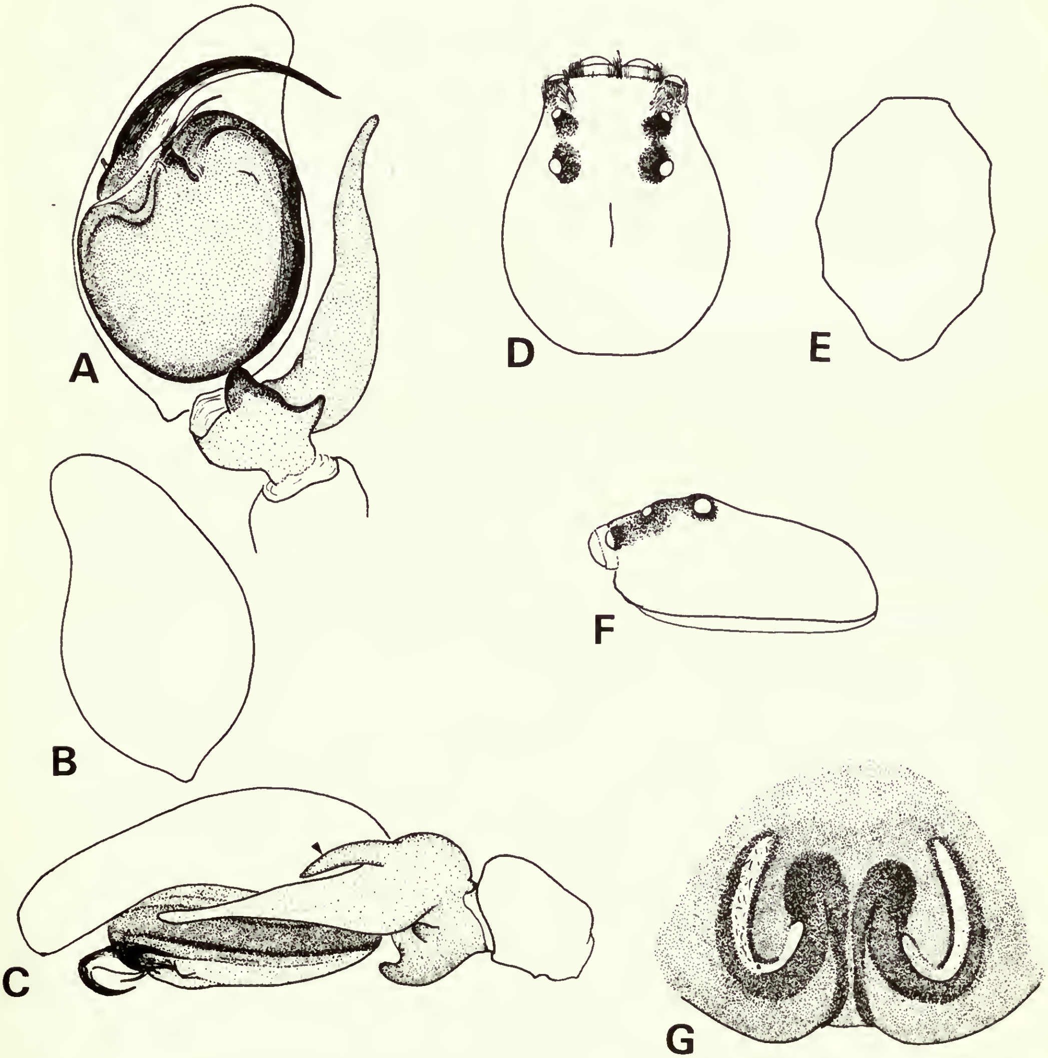

Fig. 8 *Phaeacius canalis* sp. n., ♂ holotype: A, palp, ventral view; B, palpal cymbium, dorsal view; C, palp, ectal view; D, carapace, dorsal view; E, sternum; F, carapace, lateral view. ♀ paratype: G, epigyne.

yellow. *Sternum* (Fig. 6D): pale yellow-brown, shiny; clothed in whitish yellow hairs. *Coxae*: pale yellow-brown. *Abdomen*: with two pairs of impressed spots; pale yellow-brown; clothed in yellow-brown and orange-brown hairs with scanty white tufts posteriorly; pattern essentially as in *P. malayensis* sp. n. (Fig. 7A). *Legs*: yellowish orange with obscure dark orange annuli; spines strong and numerous. Spination of legs I: metatarsi v 2–0–0, p 1–1–0, r 1–1–1, d 0–1–0; tibiae v 3–2–2, p 1–0–1, r 1–1–0, d 1–1–1; patellae p 1–0–0, r 1–0–0; femora p 0–1–1, d 0–1–3, r 0–0–1. *Palp* (Fig. 6A, B): densely clothed in whitish and dark amber hairs; secondary conductor relatively short.

Dimensions (mm): total length 9·2; carapace length 4·6, breadth 3·72, height 2·0; abdomen length 2·68; eyes, anterior row 2·22, middle row 2·0, posterior row 2·12; quadrangle length 1·7. *Ratios*: AM : AL : PM : PL : 17 : 10 : 7 : 9; AL–PM–PL : 13–15·5; AM : CL : 17–6.

Female paratype. Similar to ♂ except for the following: *Carapace*: darker; marginal band narrower and less clearly defined. *Clypeus*: clothed in light orange-brown hairs with dense covering of long white hairs in lower space between AM. *Chelicerae*: dark orange, shiny; basal region clothed in white hairs; promargin with three teeth, retromargin with five. *Legs*: spination of legs I: metatarsi v 2–0–0, p 1–1–1, r 1–1–0; tibiae v 3–2–2, p 1–1–0, r 1–1–0, d 1–1–0; patellae p 1–0–0, r 1–0–0; femora p 0–1–1, d 0–1–4. *Epigyne* (Fig. 6F): large and dark, clothed in long whitish hairs; lateral openings plugged.

Dimensions (mm): total length about 8·9; carapace length 3·76, breadth 3·04, height 1·86; abdomen length 4·8; eyes, anterior row 2·16, middle row 1·84, posterior row 1·96; quadrangle length 1·64. *Ratios*: AM : AL : PM : PL : 15·5 : 8·5; AL–PM–PL : 12–14; AM : CL : 15·5 : 5.

Distribution. Philippines.

Material examined. **Philippines:** Albay, S.E. Luzon, holotype ♂ xi–xii.1894 (*G. J. Whitehead*) (BMNH, 1895.1.17.920); Cape Engano, Paratype ♀, (*G. J. Whitehead*) (BMNH, 1897.12.24.26).

Phaeacius saxicola sp. n.

(Fig. 9A–C)

Diagnosis. *P. saxicola* is a moderately distinctive species, readily separated from others in the genus by the appearance of the epigyne (Fig. 9C).

Male. Unknown.

Female holotype. *Carapace* (Fig. 9A, B): dark orange-brown with sooty markings, also an inverted light orange-brown leaf-shaped patch on thoracic region; clothed in dull whitish and light brown hairs with white haired marginal bands and lateral dark brown haired spots. *Eyes*: with black surrounds; densely fringed in whitish and light orange-brown hairs. *Clypeus*: clothed in dull white and orange-brown hairs. *Chelicerae*: orange to brownish orange, shiny; basal region clothed in white hairs; pro and retromargins with three teeth. *Maxillae*: dark orange-brown with inner distal margins light yellowish. *Labium*: dark orange-brown tipped light yellow. *Sternum*: light yellow-brown with irregular reddish orange margins; clothed in creamy white hairs. *Coxae*: light yellow-brown. *Abdomen*: light grey with granules of yellowish guanin; rubbed, but with leaf-life pattern outlined in brown-black hairs. *Legs*: pale yellowish orange grading to orange-brown distally with indistinct annuli on metatarsi and tibiae; spines strong and numerous. Spination of legs I: metatarsi v 2–0–0, p 1–1–0, r 1–1–1; tibiae v 2–3–2, p 1–1–0, r 1–1–0, d 1–1–0; patellae p 0–1–0, r 0–1–0; femora p 0–1–1, d 0–1–4. *Epigyne* (Fig. 9C): large and dark; covered in whitish and light yellow-brown hairs.

Dimensions (mm): total length 11·3; carapace length 4·0, breadth 3·44, height 1·76; abdomen length 7·28; eyes, anterior row 2·16, middle row 1·89, posterior row 2·04;

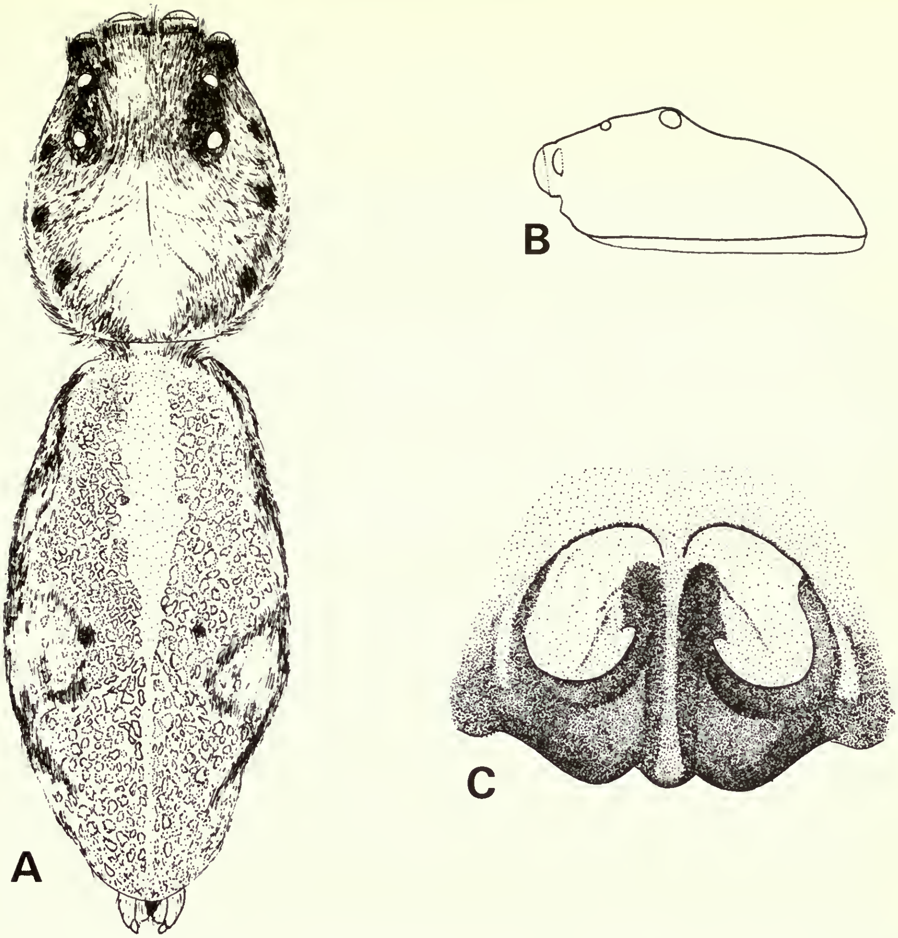

Fig. 9 *Phaeacius saxicola* sp. n., ♀ holotype: A, dorsal view; B, carapace, lateral view; C, epigyne.

quadrangle length 1·74. *Ratios*: AM : AL : PM : PL : 15·5 : 9·5 : 6 : 9; AL–PM–PL : 13–14; AM : CL : 15·5 : 4.

Distribution. Nepal.

Material examined. **Nepal**: Maewa Khola, Sanghu, holotype ♀, 6,000ft, on rock face, 10.x.1961 (*K. H. Hyatt,* British Museum Nepal Expedition, 42b) (BMNH. 1980.4.15.1).

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The protractor pectoralis muscle and the classification of teleost fishes

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Introduction

The protractor pectoralis muscle is currently thought to be one of the shared derived features characterizing certain neoteleostean fishes. Further investigation shows, however, that a protractor pectoralis muscle occurs in many taxa throughout the Teleostei, the Dipnoi, the Palaeopterygii and other lower actinopterygians, and, probably, in the Elasmobranchiomorphi as well.

Since the protractor pectoralis is apparently homologous with the trapezius muscle of tetrapods it therefore would appear to be a derived feature of the Gnathostomata as a whole and not just a synapomorphy of a group (the Eurypterygii) within the Teleostei.

In his paper on the interrelationships of the higher Euteleostei, Rosen (1973) considered the presence of a protractor pectoralis muscle to be one of the synapomorphies characterizing the section Eurypterygii of his subdivision Neoteleostei. Rosen also included in the Neoteleostei, as the primitive sister group of the Eurypterygii, the section Stenopterygii (=Stomiatiformes). Although lacking a protractor pectoralis muscle, the Stomiatiformes share other derived features with their apomorph sister taxa, *viz.* the Aulopiformes, Myctophiformes, Protacanthopterygii and Acanthopterygii (Rosen, 1973 : 505).

According to Rosen (who based his conclusions involving the protractor pectoralis largely on the then unpublished work of Winterbottom) this muscle does not occur in any other group of teleostean fishes. When that work was published the following year, Winterbottom (1974 : 269) repeated the claim that '... the protractor pectoralis appears to be confined to the neoteleosts', despite the fact that he described and illustrated the muscle in three non-neoteleostean taxa, the ostariophysans *Brycon, Cyprinus* and *Diplomystus.*

This *lapsus* is probably explained by Winterbottom's definition of the concepts 'neoteleosts' and 'non-neoteleosts' (Winterbottom, 1974 : 227). He uses the term neoteleost '... in the sense proposed by Rosen & Patterson (1969 : 460)' but uses its antithesis, the non-neoteleosts, '... to designate Divisions I and II, and the salmoniforms (less myctophoids) of Division III of the Greenwood *et al.* (1966) classification'. Thus the Ostariophysi and the Gonorynchiformes of Greenwood *et al.* were left in limbo, neither neoteleosts nor non-neoteleosts, and were overlooked.

A further complication is introduced by Winterbottom's report in some clupeomorphs (*sensu* Greenwood, Rosen, Weitzman & Myers, 1966) of a muscle which, in his opinion (1974 : 269) '... seems to be analogous to the protractor pectoralis', and with which '... the muscle in the neoteleosts would appear to be a homologous structure, and indicative of common ancestry'.

These incongruities in recently published accounts, coupled with the fact that a muscle apparently identical to the protractor pectoralis in neoteleosts has been described in

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chondrichthyans (=Elasmobranchiomorphi), dipnoans and non-teleostean actinopterygians (see Allis, 1917; Edgeworth, 1911 & 1935), led us to review and reconsider the value of this muscle as a character in reconstructing gnathostome phylogenies, especially those of teleostean fishes.

As a first step we have reviewed the literature dealing with the protractor pectoralis (*ie* essentially the cucullaris and cephaloclavicularis muscles of Edgeworth and the trapezius of Allis) in lower gnathostomes, and have compared these findings with our dissections covering a wider range of taxa than any previously examined (see Table 1).

Allis (1917 : 343–350, and 402) gives a detailed summary of the situation at that time with respect to gnathostome fishes, and includes a critique of Edgeworth's earlier (1911) paper, the only wide-ranging review of cranial musculature in vertebrates then available. Later, Edgeworth (1935) expanded his earlier essay. Apart from these three works, and Winterbottom's (1974) recent contribution, there are no other papers dealing with the prime question we wished to review, namely the homology of the protractor pectoralis both within and outside the teleostean fishes.

Allis (1917) concludes that amongst gnathostome fishes the protractor pectoralis (his trapezius) is always innervated by the vagus, and that it is derived, embryologically, from the muscle plate of the last branchial arch. Thus, at least implicitly, Allis would consider the muscle to be homolgous in these animals. Edgeworth (1911; 1935) reaches a similar conclusion regarding the muscle's homology, and extends it even beyond the limits of the gnathostome fishes. According to Edgeworth (1935 : 151) the protractor pectoralis (which he calls cucullaris) 'In Dipnoi, Teleostomi, Amphibia, Reptilia and Mammalia . . . is developed as a backgrowth of the most caudal branchial muscle plate', and more specifically, (p. 151), 'The similar primary innervation of the Cucullaris from the most caudal fibres of the Vagus shows that the muscle has had a continuous phyletic history and is to be regarded as a homologous structure whatever its source'.

Ontogenetically, Edgeworth considered that in Dipnoi and other teleostomes the protractor pectoralis is derived from the posterior margin of the levator arcuum branchialium anlage (which would be topologically equivalent to Allis' muscle plate of the last branchial arch). However, in the Elasmobranchiomorphi (except the rays, Batoidei), he believed that the muscle is formed from the dorsal ends of all the embryonic branchial muscle plates (*ie* the embryonic branchial constrictors since in these animals no levator muscles are differentiated; see Edgeworth, 1935 : 232–233). In the Batoidei, according to Edgeworth, the protractor develops from the dorsal end of the fifth muscle plate alone, a condition which he thought was '. . . probably secondary to that in the Selachii and without any genetic relationship to that of the Teleostomi' (see Edgeworth: 152, and also 140 & 142). In other words, the batoid condition was derived from the selachian one which, in turn, Edgeworth considered to be derived from that basic to the gnathostomes, and characterized by the failure of the levator muscles to develop from the branchial muscle anlage (Edgeworth, 1911 : 193; 1935 : 152).

Allis (1917 : 346–7) contested Edgeworth's general conclusions (first published in 1911) regarding the derivation of the protractor pectoralis in elasmobranchiomorphs. In his opinion (based on personal observations and the literature available) the muscle in selachians '. . . is simply a differentiation of the constrictor superficialis of the ultimate branchial arch'. Allis took further support for his views from Dohrn's (1884; 1885) failure to find that the muscle in selachians was developed from the dorsal ends of all the branchial muscle plates.

This discrepancy between the viewpoints of Allis and Edgeworth has, as far as we can determine, never been resolved. It is of interest to note that in Edgeworth's 1935 account of the muscle and its development he entirely ignores Allis' comments. In part, their difference in viewpoints may be attributable to the fact that Edgeworth's approach was primarily embryological whilst Allis' first-hand information was derived from the dissection of post-embryonic fishes. Further and more critical work needs to be done before the problem can be resolved.

Until this uncertainty has been eliminated we must have some reservations about accepting the homology of the protractor pectoralis in elasmobranchiomorphs with the muscle identified as the protractor pectoralis in lower Teleostomi.

As far as the teleostome fishes are concerned, the results of both Allis' and Edgeworth's reviews strongly indicate the homology of the muscle throughout the group, at least with respect to those members of the Dipnoi and Actinopterygii which they had studied or which had been reported upon by others.

Winterbottom (1974 : 269) has clarified the confusion surrounding Edgeworth's (1935 : 131 & 143) account of the muscle in teleosts, especially the confusion stemming from his use of two names for a morphologically identical muscle. From our own experience we would endorse fully the conclusions reached by Winterbottom, and we therefore also treat Edgeworth's cucullaris and cephaloclavicularis muscles as synonymous, and thus, in turn, as a synonym of Winterbottom's protractor pectoralis muscle. We have also been able to check and clarify certain claims for the absence of the muscle, made by Allis (1917) and Vetter (1878). These are discussed below (p. 228).

None of our anatomical investigations on post-larval specimens would seem to refute the hypothesis that the protractor pectoralis muscle is homologous throughout the lower gnathostomes (with, of course, the reservations noted above regarding that muscle in the Elasmobranchiomorphi). We are very conscious that our research has only involved an investigation of post-embryonic material; the absence of detailed ontogenetic studies is a serious drawback in any attempt to investigate homologies.

Since Winterbottom (1974 : 269) expressed some uncertainty about the homology of the muscle he called the protractor pectoralis in the Clupeomorpha, that problem will be considered now.

Our observations (Table 1), based on 21 non-engraulid clupeoid taxa (the muscle apparently is absent in engraulids), lead us to believe that Winterbottom's difficulty stems partly from his mis-identification of a muscle as being entirely the fourth levator externus, and partly from the extreme postero-lateral displacement of the origin for the protractor pectoralis and consequently its very close association with the cranial insertion point of some epaxial body muscles (see Fig. 3).

We agree with Winterbottom in identifying the thin, strap-like muscle, running from the pterotic to the shoulder girdle, as the protractor pectoralis (see Winterbottom, 1974, fig. 24). But, we would identify the usually thin, sheet-like but somewhat expanded muscle lying ventral to it as the levator posterior muscle and not, as he does, a muscle composed entirely of the expanded 4th levator externus; we have not found, even in *Clupea harengus,* such an expansive and continuous muscle sheet lying between the protractor pectoralis and the main levator muscle mass as is shown in Winterbottom's figure 24. In other words, we believe that Winterbottom included the posterior levator, the 4th levator externus, and some non-muscular tissue lying above and between these muscles, in the 'muscle' he identified as the 4th levator externus.

In the clupeoids we examined, the protractor pectoralis and the levator posterior share a common site of origin and often a common tendon of attachment to that site. Both muscles are closely apposed to the surface of the epaxial body muscles which lie dorsal and medial to them, and both are often difficult to locate.

The clupeoid fourth levator externus muscle is much thicker and more nearly spindle-shaped than are the protractor pectoralis and posterior levator muscles. Its origin is contiguous with those of the other levators and is thus well separated from the origin of the posterior levator. It inserts on the dorso-medial angle of the enlarged 4th epibranchial. In contrast, the posterior levator inserts broadly along and behind almost the entire dorsal margin of that epibranchial.

As in many other teleosts, the origin of the presumed protractor pectoralis in clupeoids is closely associated with the origin of the levator posterior, the muscle is well separated from the origins of the levatores externi and interni muscles, and it inserts onto the cleithrum. We therefore consider that, within the terms of reference available to us and other workers, the muscle in clupeomorphs is homologous with the muscle identified as a protractor pectoralis in other teleosts.

Clearly, the presence of a protractor pectoralis muscle cannot be taken as a synapomorphy for the eurypterygian neoteleosts (see Rosen, 1973), a conclusion which is supported by evidence from many other taxa, and which will be discussed further below (p. 232). Parenthetically we note that the interrelationships of the protractor pectoralis and the levator posterior muscles have been the cause of confusion on previous occasions, as is shown by Winterbottom's (1974 : 269) lucid unravelling of that problem in Edgeworth's account of the so-called cucullaris and cephaloclavicularis muscles (Edgeworth, 1935 : 131–143).

Materials and methods

The comparative anatomy of the protractor pectoralis muscle was examined in over 250 taxa of primitive gnathostomes. In Table I we list the species examined, the presence or absence of the protractor pectoralis in each taxon, an indication of whether further comments on the anatomy will be given in the text (see pp. 222–232), and the register number(s) for the specimen(s) examined. All specimens are from the British Museum (Natural History) fish collection unless otherwise noted: the abbreviation 'MCZ' before a number indicates a specimen in the collection of the Museum of Comparative Zoology, Harvard University, and 'I.O.S.' refers to the Institute of Oceanographic Sciences' *Discovery* collection station number. A figure in parenthesis after the register numbers indicates the number of specimens which were examined from that particular lot.

The protractor pectoralis muscle is often extremely thin, and great care must be exercised when dissecting to prevent accidental removal of the muscle. In particular, removal of gill filaments from the arches, and the superficial fascia covering the dorsal branchial muscles laterally, should be done with caution. Portions of the pectoral girdle, especially the posttemporal, supracleithrum, and dorsal aspect of the cleithrum, were often removed to enable obliquus superioris muscle fibres to be distinguished from those of the protractor pectoralis.

The muscle nomenclature in this paper follows that of Winterbottom (1974) because of its general acceptance by investigators of teleostean morphology. We realize, however, that in studies of other basal gnathostome groups use of the term 'trapezius' has become common for a muscle which we consider to be homologous with the protractor pectoralis.

Taxon	Protractor pectoralis		Annotations in text (pp. 222–232)	Register number
	Present	Absent		
ELASMOBRANCHIOMORPHI			+	
Centrophorus sp. (embryo)	+			1973.7.12 : 18–21
Hexanchus sp. (embryo)	+			1973.7.12 : 1–3
Scyliorhinus caniculus	+			1961.10.10 : 1–11
ACTINISTIA			+	
Latimeria chalumnae		+		BMNH uncatalogued
DIPNOI			+	
Neoceratodus forsteri	+		+	1959.8.11 : 12
Protopterus aethiopicus	+		+	1957.6.11 : 1–4
ACTINOPTERYGII				
Acipenseriformes				
Acipenser schrencki	+		+	1925.8.6 : 3
Polypteriformes				
Calamoichthys calabaricus	+		+	1894.7.30 : 14–15
Polypterus bichir		+	+	1928.7.3 : 1
Polypterus ornatipinnis	+		+	BMNH uncatalogued
Polypterus senegalus		+		1969.3.17 : 1–3

Table 1 cont.

Taxon	Protractor pectoralis Present	Protractor pectoralis Absent	Annotations in text (pp. 222–232)	Register number
GINGLYMODI				
Lepisosteus oculatus		+	+	MCZ 34650
Lepisosteus osseus		+	+	MCZ uncatalogued
HALECOMORPHI				
Amia calva	+		+	MCZ uncatalogued
TELEOSTEI				
Osteoglossomorpha			+	
Arapaima gigas		+		BMNH uncatalogued
Brienomyrus taverni		+		1976.10.12 : 299–302
Gnathonemus longibarbis		+		1971.6.22 : 20–27
Gymnarchus niloticus		+		1953.7.10 : 5
Heterotis niloticus		+		1969.3.26 : 43
Hiodon tergisus		+	+	BMNH uncatalogued
Hyperopisus bebe		+		1971.9.28 : 28
Mormyrops deliciosus		+		MCZ 50425
Mormyrops engystoma		+		1976.5.21 : 1–4
Mormyrus kannume		+		BMNH uncatalogued
Mormyrus macrophthalmus		+		1971.9.28 : 15–18
Notopterus kapirat		+		BMNH uncatalogued
Pantodon buchholzi		+		BMNH uncatalogued
Papyrocranus afer		+		1969.3.26 : 27
Papyrocranus afer		+		1977.11.8 : 16–18
Petrocephalus catostoma		+		1976.3.18 : 2372–2390
Scleropages formosus		+		1962.9.5 : 2–6 (2)
Xenomystus nigri		+		BMNH uncatalogued
Elopomorpha				
Albula vulpes		+		MCZ 18064
Albula vulpes		+		1955.9.19 : 875–878
Anguilla anguilla		+		1962.6.29 : 11–42
Elops hawaiensis		+		1962.4.3 : 1–25
Elops machnata		+		1962.3.26 : 1–8
Halosaurus guentheri		+		1966.10.14 : 1–2
Megalops atlanticus		+		BMNH uncatalogued
Nemichthys scolopaceus		+		1968.3.2 : 1
Notacanthus bonaparti		+		1973.10.29 : 161–183
Clupeomorpha			+	
Alosa pseudoharengus	+			1974.6.25 : 540–559
Alosa pseudoharengus	+			MCZ uncatalogued
Anchoa hepsetus		+		1974.6.26 : 1916–1945
Anchoa spinifer		+	+	1974.6.26 : 947–956
Anchoa spinifer		+		1974.7.29 : 10–13
Brevoortia tyrannus	+			1974.7.26 : 60–84
Chirocentrus dorab	+		+	1966.11.16 : 3–4
Clupea harengus	+		+	1970.2.17 : 2–20
Cynothrissa mento	+		+	1967.12.29 : 1–79
Denticeps clupeoides		+	+	1969.4.28 : 1–4
Dorosoma cepedianum	+			1974.7.20 : 90–95
Dussumieria acuta	+			1935.9.20 : 1–8
Dussumieria hasseltii	+			1964.12.14 : 1–24
Engraulis edentulus		+		1976.4.30 : 14–19

Table 1 cont.

Taxon	Protractor pectoralis		Annotations in text (pp. 222–232)	Register number
	Present	Absent		
Engraulis japonica		+		1969.4.22 : 1667–1676
Etrumeus teres	+			1974.6.19 : 4–11
Gilchristella sp.		+		1973.2.9 : 1–30
Jenkinsia stolifera		+		1972.5.4 : 55–56
Nematalosa come	+			1974.5.25 : 21–26
Neopisthopterus sp.		+		1974.7.11 : 559–578
Odontognathus panamensis	+			1974.6.26 : 7–9
Odontognathus panamensis	+			1974.7.11 : 79–123
Opisthopterus dovi	+			1974.6.26 : 139–147
Pellonula afzeliusi		+		1970.9.24 : 64–83
Sardinella jussieu	+			1966.11.16 : 20–27
Sprattus sprattus	+			1939.2.21 : 5–7
Stolephorus commersonii		+		1969.4.22 : 333–341
Stolephorus indicus		+		1969.4.22 : 2–6
Stolephorus heterolobus		+		1967.11.13 : 310–318
Ostariophysi			+	
Anotophysi				
Chanos chanos	+		+	1964.12.18 : 382
Chanos chanos	+			MCZ uncatalogued
Gonorynchus gonorynchus	+		+	BMNH uncatalogued
Phractolaemus ansorgii	+		+	1979.3.5 : 217–219
Otophysi				
Cypriniformes				
Abramis brama		+		1974.9.5 : 1–31
Aspius vorax		+		1920.1.22 : 127–146
Barbus barbus	+		+	1864.4.11 : 41–42
Barbus intermedius australis		+	+	1980.4.18 : 79–83
Barilius bendelisis		+		1970.12.14 : 208–228
Capoeta capoeta		+		1958.11.7 : 7–10
Carassius auratus	+			1973.1.22 : 91–100
Catostomus commersonii	+			1973.1.22 : 41–44
Cobitis caspia romanica	+			1957.12.9 : 293–297
Cyprinus carpio	+		+	1977.7.19 : 1–4
Cyprinus carpio	+			MCZ uncatalogued
Gyrinocheilus aymonieri	+			1957.2.26 : 8–107
Noemacheilus barbatulus	+			1969.6.12 : 13–24
Notemigonus crysoleucas		+		MCZ uncatalogued
Opsariichthys uncirostris	+			1923.3.5 : 6–12
Opsariichthys uncirostris	+			1902.5.30 : 45–54
Opsaridium ubangensis	+			1978.8.3 : 59–113
Oxygaster anomalura		+		1978.9.5 : 5–7
Rutilus rutilus		+		BMNH uncatalogued
Tinca tinca	+			1970.9.24 : 238–240
Characiformes				
Alestes nurse	+			BMNH uncatalogued
Alestes rutilus	+			1977.11.16 : 25–35
Brycon dentex	+			MCZ uncatalogued
Brycon falcatus	+			1972.10.17 : 1398–1411
Erythrinus erythrinus	+			1971.11.26 : 5–7
Hoplias malabaricus	+			1974.5.22 : 154–173
Pyrrhulina filamentosa	+			1926.3.2 : 74–90

Table 1 cont.

Taxon	Protractor pectoralis		Annotations in text (pp. 222–232)	Register number
	Present	Absent		
Gymnotoidei				
Apteronotus albifrons	+			1972.7.27 : 536–537
Gymnotus anguillaris	+			1972.10.17 : 414–423
Hypopomus artedi	+			1972.7.27 : 447–450
Siluroidei				
Arius heudeloti	+			1971.9.28 : 118–121
Diplomystes papillosus	+			MCZ 8290
Mystus cavisus	+			1976.7.1 : 32–34
PROTACANTHOPTERYGII			+	
Alepocephalus agassizii		+		1977.6.23 : 1–6
Aplochiton zebra		+		1912.12.20 : 18–19
Argentina sphyraena		+		1971.7.21 : 22–24
Argentina sphyraena		+		1970.2.17 : 87–107
Bathylagus sp.		+		1930.1.12 : 50–59
Coregonus albula		+		1906.12.5 : 1–3
Dallia pectoralis	+		+	MCZ uncatalogued
Dallia pectoralis	+			1883.12.14 : 172
Esox americanus		+		1963.2.9 : 5–9
Esox niger		+		MCZ uncatalogued
Galaxias auratus		+		1972.1.27 : 15–18
Galaxias brevipinnis	+			1964.4.30 : 32
Galaxias maculatus		+		1894.4.13 : 51–59
Galaxias vulgaris	+			1965.12.16 : 37–46
Galaxias waitei		+		1914.8.20 : 44–45
Galaxias weedoni	+			1972.1.27 : 10–14
Novumbra hubbsi		+		1965.10.19 : 17–23
Opisthoproctus soleatus	+			1934.12.19 : 1
Osmerus eperlanus		+		1979.11.26 : 11–223
Osmerus mordax		+		1963.10.28 : 16–25
Plecoglossus altivelis		+		1923.2.26 : 121
Plecoglossus altivelis		+		1965.5.2 : 43–48
Retropinna retropinna		+		1035.3.14 : 14–27
Retropinna retropinna		+		1930.2.5 : 1
Salmo trutta		+		1936.11.13 : 1–2
Thymallus thymallus		+		1979.6.22 : 226–238
Umbra krameri		+		1883.12.14 : 172
Umbra limi		+		MCZ 33124
Umbra pygmaea		+		1966.10.14 : 5–14
STENOPTERYGII				
Stomiatiformes				
Astronesthes lucifer		+		1922.6.7 : 14–23
Astronesthes niger		+		MCZ 52868
Chauliodus sloani		+		1972.2.22 : 17–19
Diplophos taenia		+		MCZ uncatalogued
Gonostoma elongatum		+		MCZ 42184
Photichthys argenteus		+		1930.1.12 : 299–306
Sternoptyx diaphana		+		1969.6.26 : 425–434
Stomias boa		+		BMNH uncatalogued

Table 1 cont.

Taxon	Protractor pectoralis		Annotations in text (pp. 222–232)	Register number
	Present	Absent		
Cyclosquamata				
Aulopiformes			+	
Aulopus filamentosus	+			1953.11.1 : 10–13
Bathysaurus agassizi	+			MCZ uncatalogued (2)
Chlorophthalmus agassizi	+			MCZ 40530
Evermanella atrata	+			I.O.S. 5420
Evermanella balbo	+			I.O.S. 7824, #24
Evermanella indica	+			I.O.S. 4947
Evermanella normalops	+			I.O.S. 7089, #24
Harpadon macrochir	+			MCZ 44232
Paralepis elongata	+			MCZ 43140
Saurida undosquamis	+			MCZ 56111
Scopelomorpha				
Myctophiformes				
Diaphus fragilis		+		MCZ uncatalogued
Electrona antarctica	+			1970.8.11 : 1–2
Gymnoscopelus aphya		+		1970.8.11 : 99–112
Lampadena speculigera	+			1962.1.3 : 11–12
Neoscopelus microchir	+			1939.5.24 : 475–483
Notoscopelus kroyeri	+			MCZ 55532
Scopelopsis multipunctatus		+		1976.9.29 : 31–32
Scopelus humboldti	+			1926.6.30 : 6–8
Paracanthopterygii				
Amblyopsis spelaea	+			1858.5.10 : 1–5
Antennarius altipinnis	+			1969.8.26 : 308–310
Aphredoderus sayanus	+			1898.12.29 : 141–149
Carapus acus	+			1952.11.25 : 1–4
Coelorhynchus occa	+			1974.6.27 : 1–6
Gadus ogac	+			MCZ 52937
Gobiesox papillifer	+			MCZ 44836
Lophius budegassa	+			1928.9.18 : 91–92
Lycodonus mirabilis	+			MCZ 38301
Malacocephalus laevis	+			MCZ 44993
Muraenolepis microps	+			1937.7.12 : 11–17
Ophiodon rochei	+			1971.12.17 : 6–8
Percopsis omiscomaycus	+			MCZ 54922
Porichthys notatus	+			MCZ uncatalogued
Porichthys porosissimus	+			1961.9.4 : 171–173
Acanthopterygii				
Atherinomorpha			+	
Anableps anableps	+			1973.9.13 : 33–36
Aphanius dispar	+			1973.9.10 : 154–194
Atherina duodecimalis	+			1974.5.25 : 3681–3697
Cyprinodon pecosensis	+			1978.8.1 : 303–502
Exocoetus obtusirostris	+			MCZ 42538
Fundulus heteroclitus	+			MCZ 51871
Lamprichthys tanganicanus	+			1955.12.20 : 1449–1465
Melanotaenia nigrans	+			1975.3.20 : 119–186
Menidia menidia	+			MCZ uncatalogued
Neostethus lankesteri	+			1970.7.22 : 71–77

Table 1 cont.

	Protractor pectoralis		Annotations in text (pp. 222–232)	Register number
Taxon	Present	Absent		
Oryzias latipes	+			1923.2.26 : 160–169
Parexocoetus brachypterus	+			1967.2.1 : 53–57
Poecilia reticulata	+			1972.9.27 : 95–129
Potamorrhaphis guianensis	+			1972.7.27 : 1014–1019
Scomberesox saurus	+			BMNH uncatalogued
Percomorpha				
Ammodytes hexapterus	+			1968.8.6 : 91–116
Anabas testudineus	+			1970.9.3 : 367–386
Archamia zosterophora	+			1974.5.25 : 1548–1560
Ariomma indicus	+			1979.7.4 : 5–8
Aulostomus chinensis	+			1960.3.10 : 7–14
Bothus podas	+			1938.11.15 : 54–55
Brachydeuterus auritus	+			1962.9.18 : 109–117
Callionymus lyra	+			1962.6.1 : 15–29
Capros aper	+			1963.5.14 : 230–239
Caranx malabaricus	+			1976.5.10 : 4–6
Centropyge bispinosus	+			BMNH uncatalogued
Congiopodus perorianus	+			1936.8.26 : 1100–1104
Cottus gobio	+			1974.9.20 : 45–55
Cyclopterus lumpus	+			1968.12.31 : 2
Dactylopterus volitans	+			1967.2.1 : 308–311
Epinephelus aeneus	+		+	1967.2.1 : 73–76
Eupomacentrus fasciolatus	+			1977.4.4 : 81–84
Gerres poeti	+		+	1974.5.25 : 2432–2436
Gobius niger	+			1971.2.16 : 1072–1081
Grammistes sexlineatus	+		+	1951.1.16 : 145–147
Gymnocephalus cernua	+			1961.4.19 : 106–115
Holocentrus spinifer	+			1960.3.15 : 170–172
Holocentrus suborbitalis	+			MCZ 43537
Hoplichthys acanthopleurus	+			1939.5.24 : 1684–1695
Hoplolatilus starcki	+		+	BMNH uncatalogued
Kutaflammeo sammara	+			1974.5.25 : 814–818
Kyphosus cuierasceus	+			1960.3.15 : 914–918
Lates microlepis	+		+	1975.8.15 : 16–33
Lepomis auritus	+			1973.1.22 : 105–112
Liparis liparis	+		+	1971.2.16 : 749–754
Lutjanus synagris	+			1976.7.14 : 209–212
Macrorhamphosus gracilis	+		+	1962.12.20 : 21–26
Mastacembelus albomaculatus	+			MCZ 49212
Monocirrhus polyacanthus	+			MCZ 46017
Monopterus albus	+		+	1976.4.2 : 77–83
Mugil cephalus	+			1975.8.15 : 204–212
Nandus nebulosus	+		+	1957.2.27 : 1–4
Notothenia larseni	+			1939.7.12
Ophioblennius steindachneri	+			1955.5.12 : 1–6
Ostichthys murdjan	+			1974.5.25 : 738–739
Pachypops fourcroi	+			1964.7.9 : 193–196
Parapercis cephalopunctata	+			1974.5.25 : 3288–3298
Pelates quadrilineatus	+			1974.5.25 : 839–855
Phanerodon furcatus	+			1979.10.16 : 16–29
Platycephalus mulleri	+		+	1974.5.25 : 4027–4028
Pleuronectes platessa	+			1971.2.16 : 1992–1993

Table 1 cont.

Taxon	Protractor pectoralis		Annotations in text (pp. 222–232)	Register number
	Present	Absent		
Polymixia nobilis	+			1862.4.22 : 17–18
Pomacanthus arctifrons	+			1938.12.12 : 90–94
Psettodes erumei	+			1933.7.31 : 1–2
Scomber japonicus	+			1967.2.1 : 41–44
Scorpaenodes insularis	+			1979.1.5 : 234–236
Sebastes crameri	+		+	1967.3.5 : 298–318
Solea solea	+			1971.2.16 : 118–127
Sphyraena chrysotaenia	+			1973.7.26 : 2–13
Stephanoberyx monae		+	+	1972.10.24 : 2–3
Synbranchus marmoratus	+		+	1925.10.28 : 24
Syngnathus acus	+			1971.2.16 : 322–327
Tautogolabrus sp.	+			BMNH uncatalogued
Thalassoma purpureum	+			1978.9.15 : 4–8
Trachipterus taenia	+		+	1891.8.31 : 27–35
Trichogaster pectoralis	+			1970.9.3 : 418–427
Uranoscopus scaber	+			1978.1.17 : 57–61
Zaniolepis latipinnis	+			1967.3.5 : 354–385
Zeus faber	+		+	MCZ 41388
Zeus faber	+			1971.7.21 : 86–90

Comments on the protractor pectoralis muscle in certain taxa

ELASMOBRANCHIOMORPHI

In selachians the protractor pectoralis (=trapezius or cucullaris of authors) originates from the fascia covering the epaxial muscles laterally (Fig. 1). The fibres extend posteroventrally to insert on the pectoral girdle. Medial to the protractor pectoralis, another muscle, which appears to be an epaxialis derivative, extends anteriorly from the dorsal aspect of the pectoral girdle to merge with epaxial muscle fibres. The fibres of this muscle lie at 90° to those of the protractor pectoralis.

Anterior to the protractor pectoralis a muscle runs posteroventrally from the epaxialis fascia to insert on the posterodorsal aspect of the last gill arch (Fig. 1). We consider this muscle to represent an anterior division of the protractor pectoralis, as did Allis (1917) and Edgeworth (1935 : 141).

The protractor pectoralis lies medial to the branchial constrictor muscles although both share a common origin from the epaxial muscle fascia. Levator arcuum branchialum muscles are absent in selachians.

ACTINISTIA

Millot & Anthony (1958 : 63, fig. 29) do not describe a protractor pectoralis muscle (or a muscle with the anatomical relationships of the protractor) in adult *Latimeria chalumnae.* We have dissected and made observations on a 32 cm foetus, and also find no trace of the muscle.

DIPNOI

Neoceratodus forsteri. The protractor pectoralis is a well-developed and distally expansive muscle (Fig. 2). Its narrow origin lies immediately posterior to the common origin of the 3rd

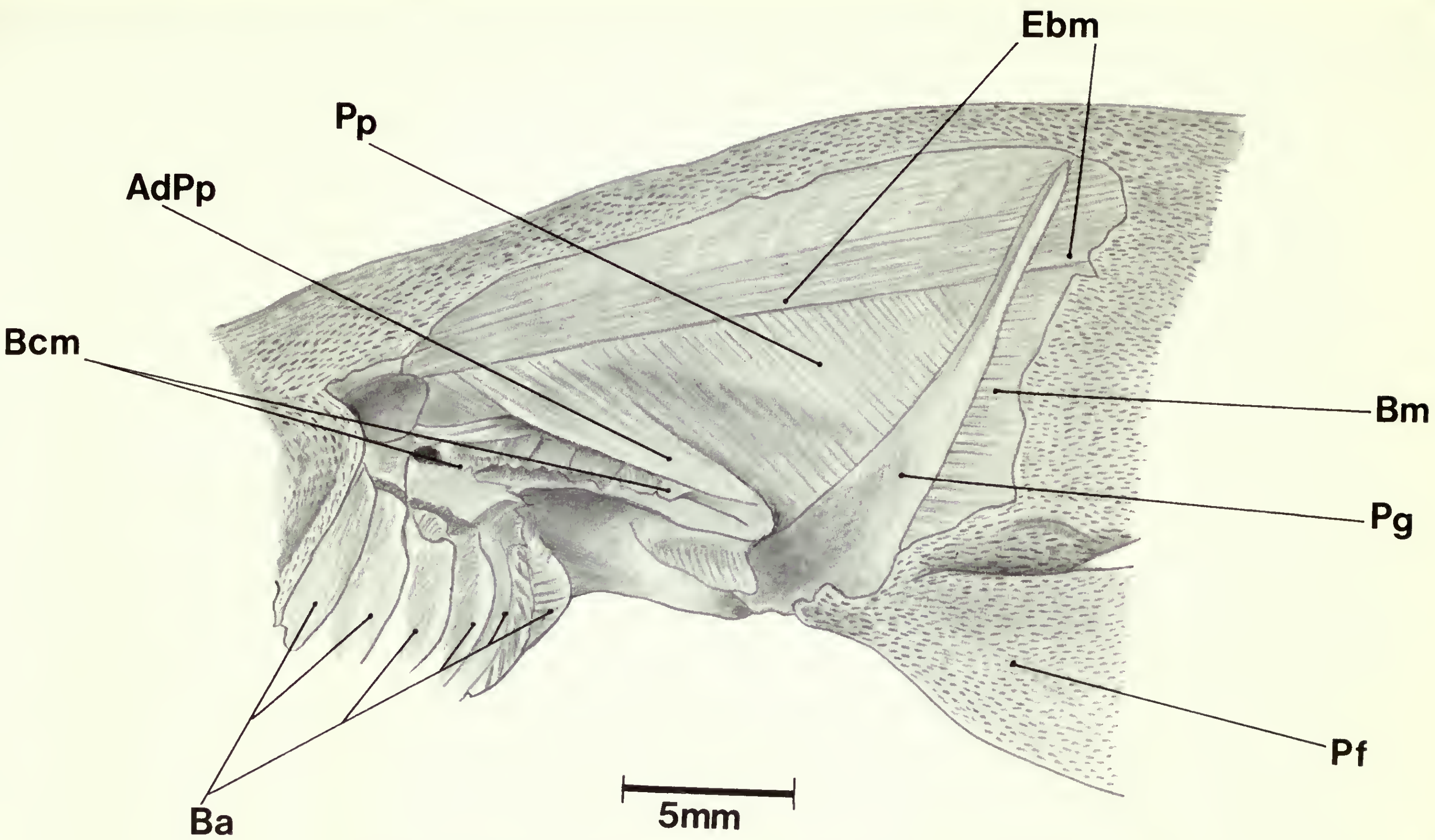

Fig. 1 *Hexanchus* sp., foetus *ca* 382 mm total length (oblique dorsolateral view, left side; first five gill arches reflected forwards). AdPp: anterior division of the protractor pectoralis muscle inserting onto 6th gill arch. Ba: branchial arches 1–6, cut dorsally and reflected forward. Bcm: cut dorsal ends of branchial muscles. Bm: body muscles. Ebm: epaxial body muscles. Pf: pectoral fin. Pg: pectoral girdle. Pp: protractor pectoralis muscle. Drawn from specimen BMNH 1973.7.12 : 1–3.

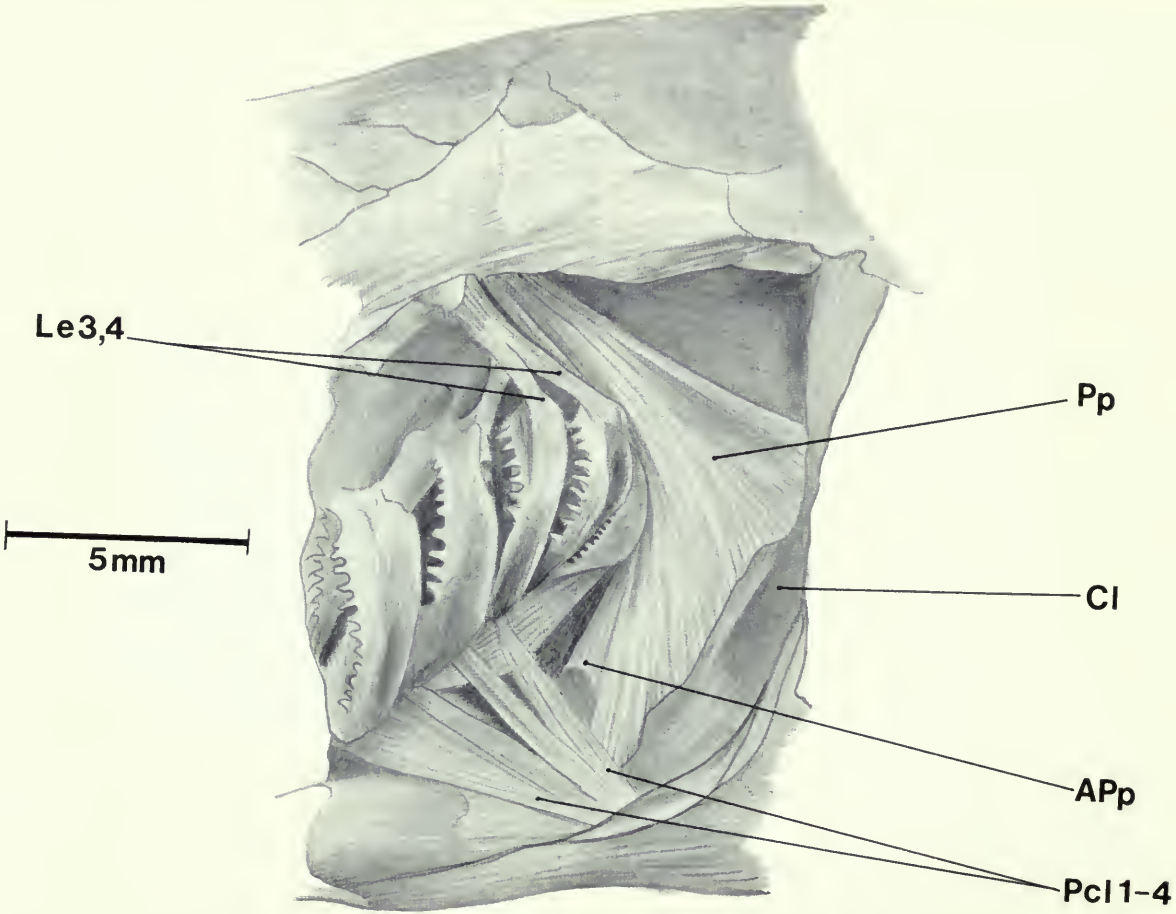

Fig. 2 *Neoceratodus forsteri* (left lateral view; gill filaments removed). APp: anterior portion of protractor pectoralis muscle (see text p. 225). Cl: cleithrum. Le3,4: external levator muscles of 3rd and 4th gill arches (those of arches 1 and 2 have been removed). PcL 1–4: pharyngoclavicularis internus muscles of gill arches 1–4. Pp: protractor pectoralis muscle. Drawn from specimen BMNH 1969.8.11 : 12.

and 4th levator externi muscles; it has a wide, musculose insertion onto the cleithrum, its antero-posterior orientation being almost in the sagittal plane.

From its apparent anterior face some fibres attach dorsally to the posterior aspect of the 5th gill arch, immediately above the origin of the subarcualis rectus of Wiley (1979 : fig. 4). Unlike Wiley, we cannot identify a separate pharyngoclavicularis internus muscle associated with the 5th gill arch. Possibly the muscle he illustrates is what, in our specimen, appears to be the anterior portion of the protractor pectoralis. In other words, the two muscles in this specimen are so closely contiguous that they give the appearance of a single muscle. The fibre orientation of this anterior muscle (if it be separate) is like that in the protractor pectoralis itself, and its attachment to the cleithrum is medial and ventral to the attachment area of the pharyngoclavicularis muscles from arches 1–4.

Protopterus aethiopicus. A protractor muscle, originating from the posterior margin of the cartilaginous skull broadens out from its narrow point of origin to insert, tendinously, on the cleithrum. The muscle, as compared with that in *Neoceratodus*, is narrow and instead of having a simple inverted fan-shape has a slightly concave and twisted anterior margin which, again unlike *Neoceratodus*, is aligned almost at right angles to the sagittal plane; posteriorly a short length of the muscle lies in that plane. Continuous with the muscle's posterior margin are several much more expansive muscle bundles. These are apparently derived from the hypaxial body musculature; dorsally the muscles attach to the horizontal septum, and posteriorly they continue beyond the girdle but give off fibres which insert on the anterior face of the cleithrum as the main muscle mass passes below that bone. Careful dissection shows that the apparent continuity of fibres from the branchial protractor pectoralis with those of the hypaxial pseudo-protractor is in fact false; the two muscles are separated by a very narrow hiatus obscured by the rather dense tissue overlying them.

ACTINOPTERYGII

Acipenseriformes

Acipenser schrencki. The very well-developed, broad and thick protractor pectoralis originates along the posterior transverse region of the skull and inserts on the cleithrum. Its origin is clearly separated from that of the muscle plate representing the levators of the 3rd and 4th gill arches.

Sewertzoff's (1928) embryological studies of the cranial muscles in *Acipenser ruthenus* clearly demonstrate the common origin of the branchial levators, and the derivation of the protractor pectoralis, from the posterior part of the same plate.

The muscle's ontogenetic history in other chondrosteans is less clear (see Edgeworth, 1935 : 142) and would repay further investigations on both embryological and adult material. According to Edgeworth *(loc. cit.)* the muscle is absent in *A. sturio* '. . . possibly by atrophy during developmental stages owing to the fixation of the pectoral girdle'.

Polypteriformes

Polypterus ornatipinnis. The protractor in this species in a thin, largely tendinous muscle which shares its origin with the 3rd and 4th levatores externi, and inserts on the cleithrum near its point of maximum curvature.

Calamoichthys calabaricus. In this species, unlike *P. ornatipinnis*, the protractor is large and noticeably broader distally than proximally. As in *P. ornatipinnis* it has a common origin with the 3rd and 4th levatores externi but inserts onto the cleithrum at a point slightly dorsal to the bone's region of maximum curvature.

GINGLYMODI

Lepisosteus osseus lacks both protractor pectoralis and levator posterior muscles. Just dorsal to the origin of the fourth levator externus, the obliquus superioris inserts tendinously on the skull. In *Lepisosteus oculatus* some lateral fibres of the obliquus superioris insert on a medial flange of the supracleithrum, but no protractor pectoralis is present.

HALECOMORPHI

Amia calva possesses a well-developed protractor pectoralis (=fifth levator externus of Allis, 1897). The protractor pectoralis originates from the otic region of the skull and inserts *via* a long tendon onto the cleithrum.

TELEOSTEI

OSTEOGLOSSOMORPHA

The osteoglossomorph fishes lack both a protractor pectoralis (Table 1) and a levator posterior muscle. Winterbottom (1974 : 252) noted that the levator posterior is confined to the neoteleosts (in his usage of the category) with the exception of *Hiodon*. We find that *Hiodon* lacks the levator posterior and possesses a posteriorly displaced origin of the fourth levator externus due to the large swimbladder extension in the otic region.

CLUPEOMORPHA

Some comments on the protractor pectoralis of clupeomorph fishes have been made already (p. 215).

In none of the clupeid and chirocentrid species we have examined is the muscle well-developed; usually it is mainly tendinous, flat and narrow, and invariably it is closely applied to the ventro-anterior face of the overlying body muscles. Often part of the protractor pectoralis inserts on the supracleithrum.

A protractor pectoralis muscle is absent in all the engraulid species examined, and apparently, in the sole extant representative of the Denticipitoidei, *Denticeps clupeoides*. However, because the only specimens of *Denticeps* available are small (*ca* 50 mm SL), a narrow, thin muscle could easily be overlooked. The muscle is present in a large proportion of the Clupeidae *(sensu lato)* we examined (Fig. 3).

A levator posterior muscle occurs in the majority of clupeomorph taxa we dissected. Its origin is shared with, or is very close to, that of the protractor pectoralis. In general it too is a thin, narrow and partly tendinous muscle, and is always closely applied to the ventro-anterior face of the body musculature (Fig. 3).

No levator posterior was found in the engraulid *Anchoa spinifer* (although the muscle is present in *A. heterolobus)*. It also appears to be absent in the chirocentrid *Chirocentrus dorab,* unless, atypically, it is closely associated with the 4th external levator muscle which, in this species, seems to be composed of two very closely contiguous parts. We are uncertain about the condition in the denticipitoids because of the small size of the available specimens.

The presence of a levator posterior in many clupeomorph fishes contradicts Winterbottom's (1974 : 252) statement about the occurrence of that muscle within the teleosts, namely, that apart from its occurrence in the osteoglossomorph *Hiodon,* it is a neoteleostean feature (see also above). It also contradicts his suggestions about a possible origin for the posterior levator from a condition like that supposedly occurring in the clupeomorphs (Winterbottom, *loc. cit.*). As noted already (p. 215), and in contradistinction to Winterbottom's observations, none of the clupeoids we examined showed any continuity of fibres between the 4th external levator and '. . . a thin sheet of muscle whose origin extends to the posterolateral tip of the pterotic' (the condition which Winterbottom considered to be the typical clupeomorph one). Our interpretation of the clupeomorph condition is that part of Winterbottom's 'thin sheet of muscle . . .' is the levator posterior muscle, but that the area of tissue between it and the 4th levator externus is devoid of muscle fibres, and consequently the two muscles are distinct from one another (see also p. 215).

OSTARIOPHYSI

A protractor pectoralis is present in some or all taxa of every otophysan subdivision (see Table 1; also Winterbottom, 1974; figs 20, 21 & 22), and apparently is absent only in certain

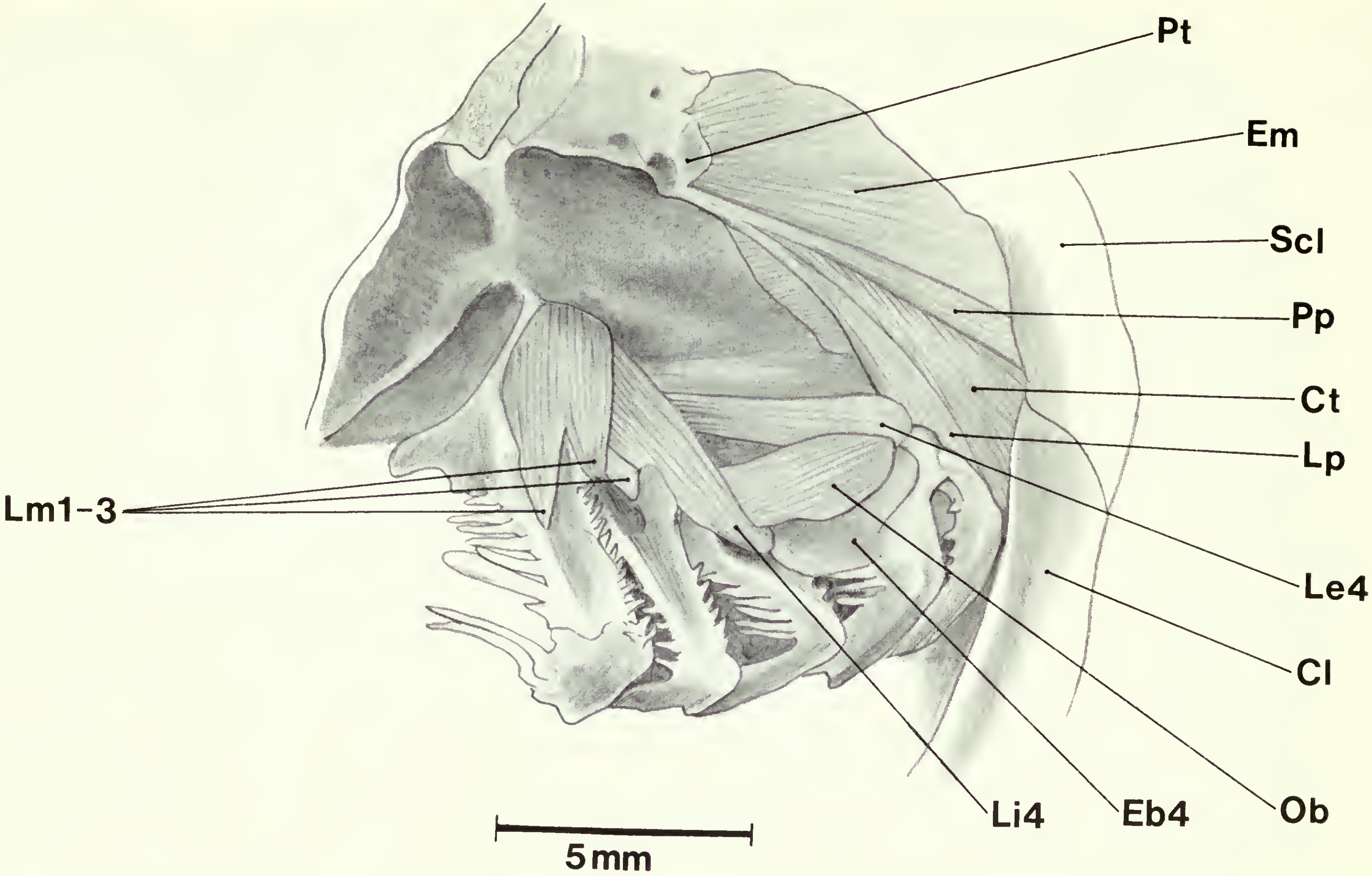

Fig. 3 *Cynothrissa mento* (slightly oblique ventrolateral view, left side; gill filaments removed). Cl: cleithrum. Ct: connective tissue overlying body musculature in posterior region of branchial cavity. Eb4: expanded 4th epibranchial bone. Em: epaxial body musculature. Le4: 4th external levator muscle. Li4: 4th internal levator muscle. Lm: 1–3: levator muscles of 1st–3rd gill arches. Lp: levator posterior muscle. Ob: obliquus dorsalis muscle. Pp: protractor pectoralis muscle. Pt: pterotic. Scl: supracleithrum. Drawn from specimen BMNH 1967.7.12.29 : 1–79.

cypriniform taxa. It is well-developed in the three members of the anotophysi we dissected, particularly in *Chanos chanos* where it is a thick, deep muscle proximally, and has a broad, tendinous insertion onto the upper half of the cleithrum; in *Gonorynchus gonorynchus* it is narrow and strap-like, inserting directly onto the girdle, while in *Phractolaemus ansorgii* it is broad, thin and partly tendinous.

Amongst those otophysans with a protractor pectoralis, the muscle, although intraspecifically constant, shows varying degrees of development; also, in some species it inserts directly onto the cleithrum, whereas in others it inserts onto the membrane extending from the girdle to form the posterior wall of the branchial chamber. When the protractor has a 'membrane insertion' it is closely applied to the anterior face of the body musculature which delimits the posterior boundary of the branchial chamber. In general, the protractor pectoralis is narrow and strap-like, and often has a near-vertical orientation.

Vetter (1878) claims that the protractor pectoralis (his trapezius), is absent in *Cyprinus carpio* and *Barbus barbus*. The muscle certainly is present in *C. carpio* (see Winterbottom, 1974, fig. 22; personal observations), but may have been overlooked by Vetter because of its slenderness and its rather tendinous nature. A short, fine, protractor pectoralis is also present in a specimen of *Barbus barbus* we dissected, although the muscle is absent in another member of that genus, *B. intermedius,* from Kenya, east Africa.

A levator posterior muscle appears to be absent in some anotophysans *(Chanos chanos)*, but is present in *Gonorynchus gonorynchus.* Its absence in *Chanos* could be correlated with the development of an expansive and complex suprabranchial organ in that genus. The muscle is seemingly also absent in *Phractolaemus ansorgii,* but the condition of our material does not permit a definite conclusion on that point.

All the otophysan taxa examined have a levator posterior muscle; it is particularly well-developed in members of the Cypriniformes (see also Winterbottom, 1974; 252–253, figs 20–22), but in other groups it is often a slender strap-like muscle.

The occurrence of a levator posterior muscle in the Ostariophysi further negates Winterbottom's claim that its presence is a neoteleostean feature (see above [Clupeomorpha], and also p. 213 regarding that author's handling of the category Ostariophysi).

Brousseau (1976*a* & *b*) has described parts of the branchial musculature in six ostariophysan taxa. It is clear from his descriptions and figures that, depending on the species involved, he has either misidentified the protractor pectoralis, or confused and compounded it with the levator posterior muscle.

PROTACANTHOPTERYGII

The distribution of the protractor pectoralis in this group is exceedingly irregular, with, in addition, the muscle occurring in relatively few taxa. As an example of its irregular occurrence, we may note its presence in some but not in other *Galaxias* species, and its presence in *Dallia pectoralis* (Fig. 4) but not in *Umbra limi, U. krameri* or *Novumbra hubbsi.*

None of the protacanthopterygian species we examined has a levator posterior muscle, and we can find no reference in the literature to its occurrence in these fishes (see also Winterbottom, 1974: 252–253).

ACANTHOPTERYGII

Lauder & Lanyon (1980: fig. 2) identified as a protractor pectoralis in *Lepomis macrochirus* a muscle inserting on the supracleithrum and posttemporal, and extending anteriorly to originate on the posterodorsal aspect of the skull. This muscle is apparently a derivative of the epaxialis and is not homologous with the protractor pectoralis as defined in this paper. The true protractor pectoralis in *Lepomis* (Fig. 5) originates dorsally from the pterotic adjacent to the origin of the levator posterior, and extends posteroventrally to fan out and insert in the connective tissue between the last gill arch and the cleithrum. No fibres of the protractor pectoralis contact the cleithrum.

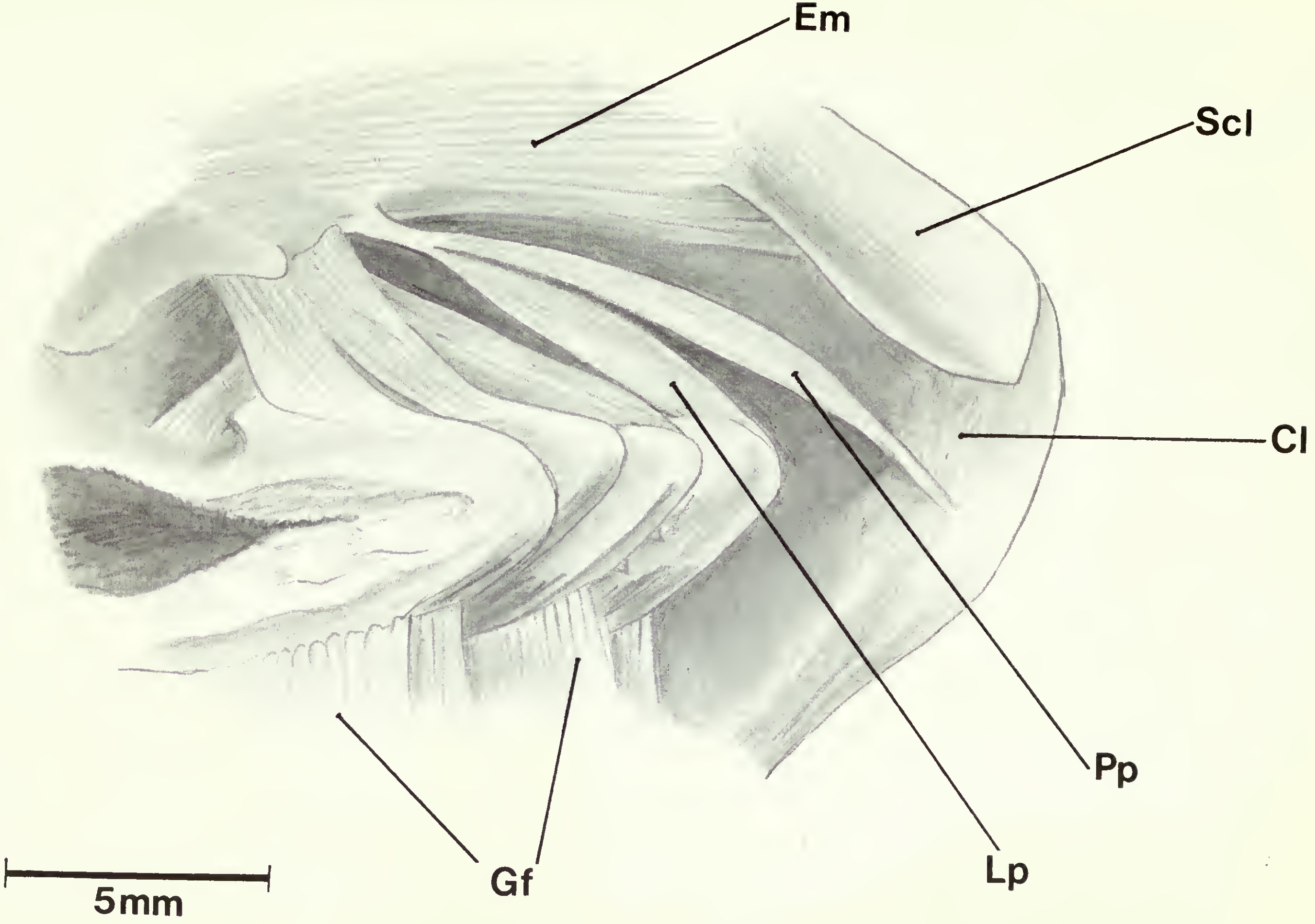

Fig. 4 *Dallia pectoralis* (slightly oblique ventrolateral view, left side, upper gill filaments removed). Cl: cleithrum. Em: epaxial body musculature. Gf: gill filaments. Lp: levator posterior muscle. Pp: protractor pectoralis muscle. Scl: supracleithrum. Drawn from specimen BMNH 1883:12.12 : 172.

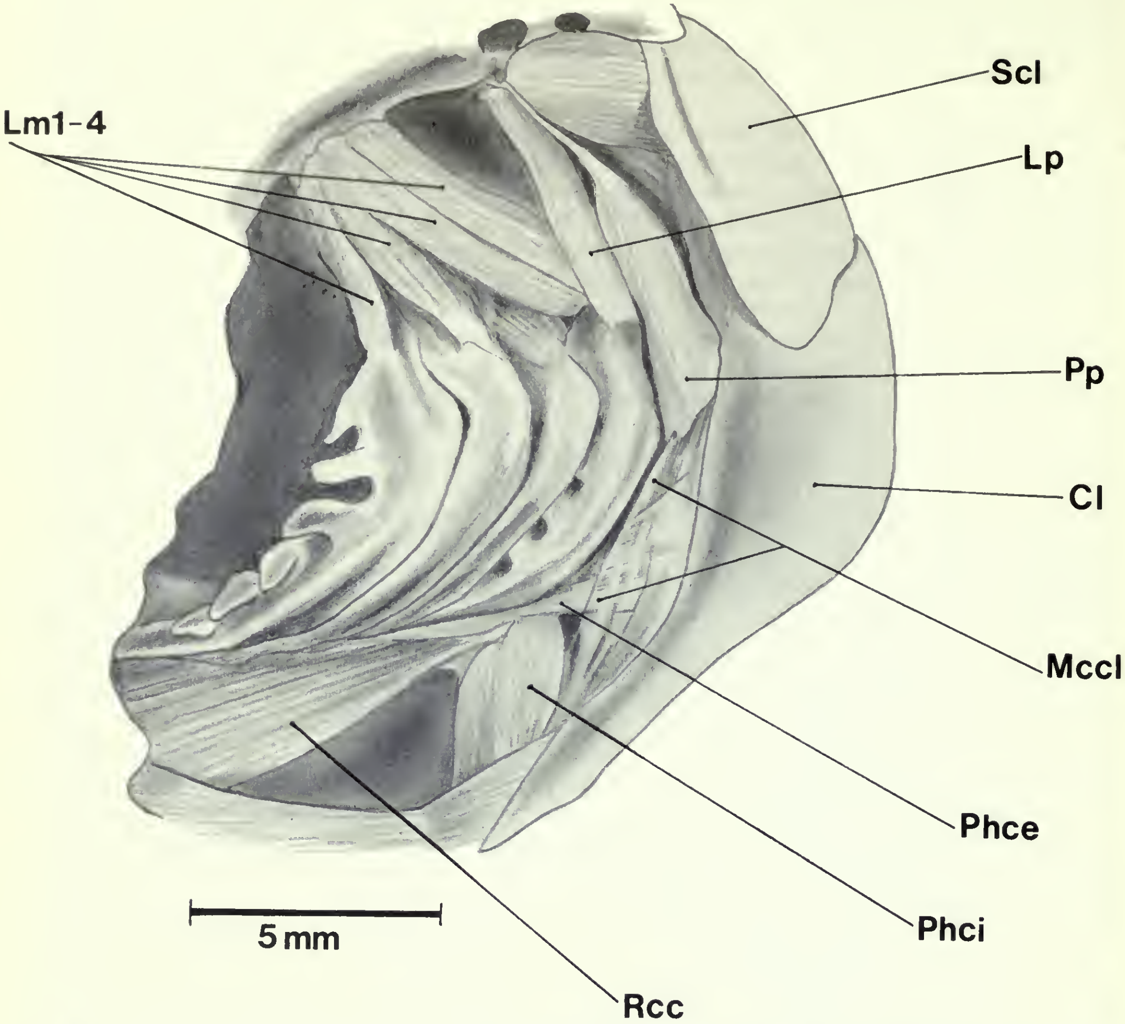

Fig. 5 *Lepomis auritus* (lateral view, left side; gill filaments removed). Cl: cleithrum. Lm 1–4: levator muscles of 1st–4th gill arches. Lp: levator posterior muscle. Mccl: membrane overlying cleithrum and distal part of pharyngocleithralis externus muscle. Phce & Phci: pharyngocleithralis internus and externus muscles, respectively. Pp: protractor pectoralis muscle. Rcc: rectus communis muscle. Scl: supracleithrum. Drawn from specimen BMNH 1973.1.22 : 105–112.

Many other acanthopterygians also possess a thin protractor pectoralis muscle which does not insert directly on the cleithrum (*eg. Zeus, Nandus, Trachipterus, Macrorhamphosus, Sebastes*). Another common condition in the Acanthopterygii is the presence of a protractor pectoralis inserting either directly onto the cleithrum (*eg.* most atherinomorphs, cichlids, *Platycephalus, Liparis, Hoplolatilus*), or inserting onto both the connective tissue posterior to the 4th ceratobranchial and the cleithrum (*eg. Lates, Epinephalus, Grammistes, Gerres*).

In both the synbranchiform taxa examined, the protractor pectoralis is, however, a well-developed, strap-like muscle running horizontally from the skull to the pectoral girdle. In *Synbranchus marmoratus* (Fig. 6) its origin is shared with that of the branchial levator muscles, and it inserts onto the small, moveable supracleithrum. An insertion onto the cleithrum itself is precluded by the position of the gill arches, which are so positioned that

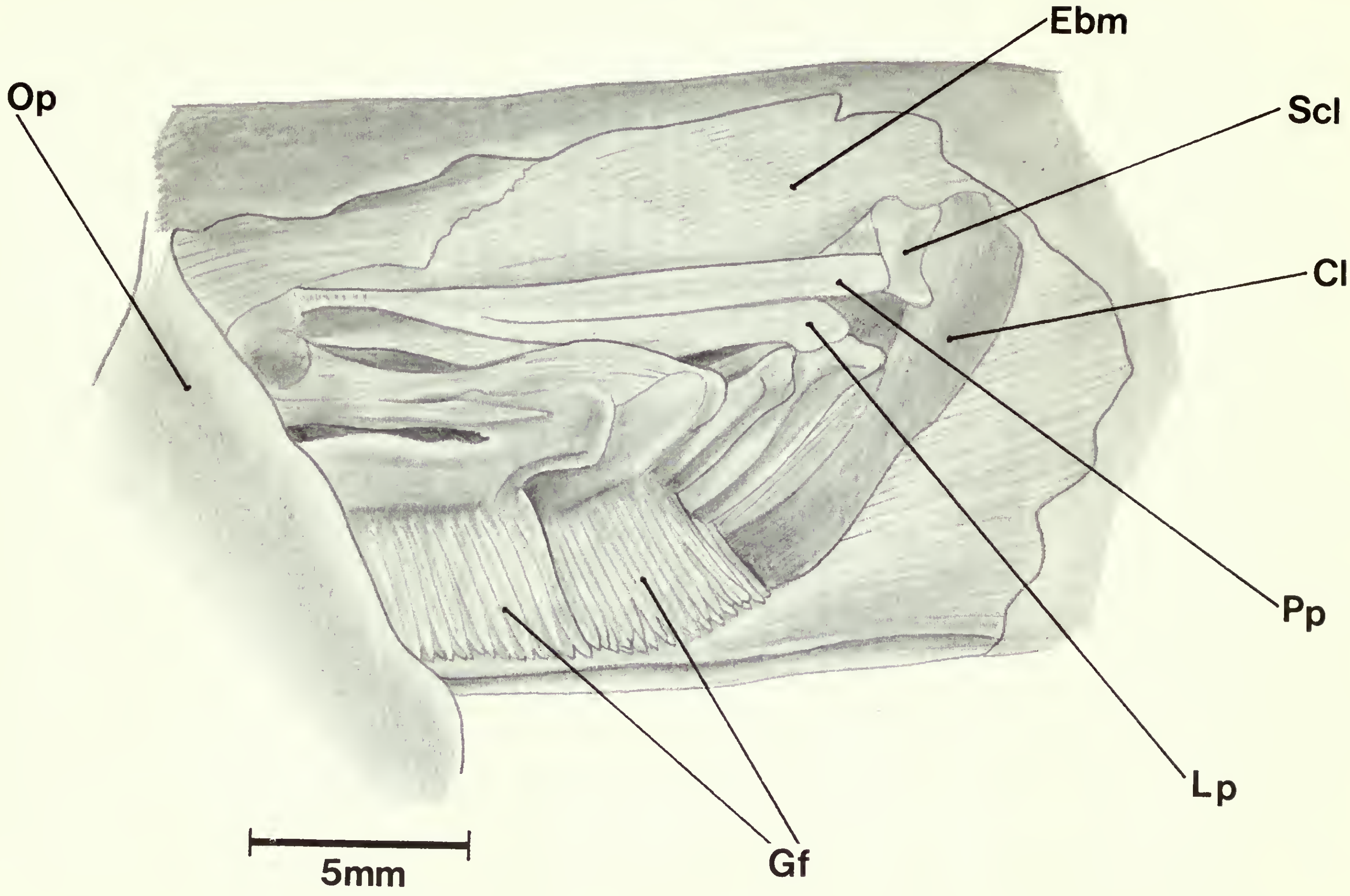

Fig. 6 *Synbranchus marmoratus* (lateral view, left side; gill filaments removed from upper parts of gill arches). Cl: cleithrum. Ebm: epaxial body muscles. Gf: gill filaments. Lp: levator posterior muscle. Op: opercular bones and membranes reflected forward. Pp: protractor pectoralis muscle. Scl: supracleithrum. Drawn from specimen BMNH 1925.10.28 : 24.

the path of the protractor is directed so as to lie above the dorsal extremity of the cleithrum. The origin of the protractor in *Monopterus albus* lies posterior to and well-separated from that of the levators, and its orientation is such that it inserts onto the dorsal tip of the cleithrum. The dorsoposterior margin of the protractor pectoralis is closely applied to the ventral margin of the supracleithrum, but no fibres from the muscle are inserted onto the bone.

The muscle in *Lepomis* identified by Lauder & Lanyon (1980, fig. 2) as a protractor pectoralis (see above), is of uncertain homology. It appears to be similar to the levator pectoralis of Winterbottom (1974: 270, and fig. 25) which has been found in batrachoids, lophiids, and tetraodontiforms. We have also found a similar muscle to the levator pectoralis in scorpaeniforms and nandids, and it may have a much wider distribution than is presently realized.

Summary and conclusions

Since our interest in the protractor pectoralis was stimulated initially by irregularities in its presumed phylogenetically based pattern of distribution within the Teleostei (see p. 213), our principal concern is with the effects additional data have on the phylogenetic conclusions reached previously (Rosen, 1973; Winterbottom, 1974).

Clearly, because of its occurrence in some or even many members of the Clupeomorpha, Ostariophysi and Protacanthopterygii, the protractor pectoralis is not, as was once thought, a feature restricted to the Neoteleostei (see pp. 217–219). Indeed, its overall pattern of occurrence extends beyond the current limits of the Euteleostei (of which the Neoteleostei are a major subdivision; Rosen, 1973; Patterson & Rosen, 1977) to include the Teleostei (*sensu* Patterson & Rosen) as a whole.

Taking the argument further: if one accepts the supposed homology of the muscle throughout the gnathostomes, the protractor pectoralis occurs in some or all members of the Neopterygii, Palaeopterygii, Dipnoi and, very probably, the Elasmobranchiomorphi as well (see pp. 214; 216–221). Amongst the major groups making up the lower gnathostomes, a protractor pectoralis is absent only in the extant Actinistia, a group represented by the single taxon *Latimeria chalumnae*.

The protractor pectoralis, therefore, would seem to be a synapomorphy of the Gnathostomata and thus, within the various lineages of that group, its presence must be treated as a plesiomorph character and not as a synapomorphy of the Teleostei in part.

Its distribution among the lower gnathostomes has a somewhat patchy pattern (see Table 1), a pattern whose patchiness is, in some respects, even more marked and more puzzling within the Teleostei.

A protractor pectoralis is not developed in the two lineages which are generally thought to be the most primitive amongst living teleosts, namely the Osteoglossomorpha and the Elopomorpha. Patterson & Rosen (1977) for example, consider the Osteoglossomorpha to be the plesiomorph sister group of all other living teleosts combined (*ie* the Elopocephala), and the Elopomorpha to be the plesiomorph sister group of the other Elopocephala (*ie* the Clupeocephala). The muscle is also absent in one 'higher' group, the Stomiatiformes, which, on the basis of its having certain derived characters, Rosen (1973: 505) identified as the plesiomorph sister group of all other lineages he brought together as the Neoteleostei (see also p. 213). Within those other lineages (*ie* the Aulopiformes, Myctophiformes, Paracanthopterygii and Acanthopterygii) a protractor pectoralis has been found in virtually all taxa placed in the supposedly 'higher' categories Paracanthopterygii and Acanthopterygii,[1] in the majority of Aulopiformes, and in many Myctophiformes as well (See Table I; also Winterbottom, 1974).

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[1] The exceptional taxon is *Stephanoberyx monae;* no protractor was found in the two specimens we examined.

Among lineages which lie, cladistically speaking, between the plesiomorph Osteoglossomorpha + Elopomorpha on the one hand and the apomorphic Neoteleostei (*sensu* Rosen) on the other, the muscle occurs in most members of the Clupeomorpha and in many Ostariophysi (including the plesiomorphic Anotophysi), but is found in only a few members of the Protacanthopterygii.

An intriguing aspect of this pattern is the contrast between the absence of a protractor pectoralis (a derived condition) in the two most primitive lineages, and its presence (the primitive condition) in the more derived ones. Equally intriguing is the way the muscle, in taxa belonging to the 'intermediate' groups, may be absent in some species of a genus but not in others (for example in the protacanthopterygian genus *Galaxias*), or in some but not all members of seemingly closely related taxa (for example, again amongst the protacanthopterygians, its presence in *Dallia,* but its absence in *Umbra* and *Novumbra*). Similar patterns of presence or absence can be found within the Clupeomorpha and the Ostariophysi (see Table 1).

We can offer no explanation for these patterns, and must conclude that the presence or absence of a protractor pectoralis muscle is a feature of little value as an indicator of phyletic relationship except at a high level of universality. In other words, it is a synapomorphy of the Gnathostomata.

Within the Teleostei we are impressed by the constancy of its presence in the Paracanthopterygii and Acanthopterygii, and by the constancy of its absence in some other groups (for example, the Osteoglossomorpha). This pattern would suggest to us that in these lineages the ontogenetic canalization leading either to the development or to the suppression of a protractor pectoralis was fixed very early in the history of each lineage. In contrast, the irregular patterns seen in other lineages (for example the Ostariophysi and Protacanthopterygii) would seem to indicate the retention of a flexible linkage between the pathway of protractor pectoralis ontogeny and other elements of the total ontogenetic pattern. What significance, if any, this may have in tracing phyletic histories remains obscure.

All our conclusions (and speculations) are, of course, dependent on the hypothesis that the muscle is an homologous (*ie* synapomorphic) feature within the Gnathostomata. Our investigations provide no refutation of that hypothesis, but we are of the opinion that the only critical test will come from comparative embryological and ontogenetic studies on a larger scale than has been carried out so far.

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We are most grateful for the assistance given to us by our colleagues in the Museum of Comparative Zoology and the British Museum (Natural History), especially Karel Liem, William and Sara Fink, Keith Banister and Gordon Howes (who also drew the figures).

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The ostracod genus *Loxoconcha* Sars from Abu Dhabi lagoon and the neighbouring near-shore shelf, Persian Gulf

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Introduction

The present study on the genus *Loxoconcha* from the region of Abu Dhabi lagoon (Lat. 24° 32′ N, Long. 54° 27′ E), follows a number of ecological and taxonomic papers (see Bate 1971, 1973; Bate & Sheppard, 1980; and Gurney 1979*a* & *b*) that have been based on material collected by Dr Graham Evans of Imperial College, London, during the period 1961–65. This material, collected during an investigation of the Recent sediments of the Trucial coast, has been supplemented, for the ostracod studies, with samples collected by Professor John Murray (Exeter) in 1969.

Elsewhere in the Gulf, Sabeekah Razzaq (1979) has undertaken a preliminary study of the benthic microfauna of Kuwait while Paik (1976 & 1977) has examined the ostracod faunas on the Iranian side of the Gulf as well as from the Gulf of Oman. Other papers relevant to our study are those of Hartmann 1964, on ostracods from the Red Sea; Jain 1978, on the fauna of Mandvi Beach, west coast of India and Bhatia 1979, on part of the fauna from off Karwar, west coast of India.

Four species of *Loxoconcha* (*Loxoconcha*) and one of the new subgenus *Epakroconcha* are described here; it is the purpose of this paper not only to place these on record but to discuss the relevance of the ornamental differences (ranging from coarsely reticulate to finely pitted) that are exhibited between the species.

Systematic descriptions

Genus *LOXOCONCHA* Sars, 1866

Remarks. In Bate *et al.* (in press), the genus *Loxoconcha* was divided into two subgenera: *Loxoconcha* and *Loxocorniculum*. Here a third subgenus *Epakroconcha* is recognized. Of the five species described from Abu Dhabi lagoon and the Persian Gulf, four belong to the subgenus *Loxoconcha*, being forms having a clear cut dimorphism of subquadrate females and subrectangular males. The fifth species differs by having a subtrigonal outline for both males and females and is accordingly placed in the separate subgenus *Epakroconcha*.

Subgenus *LOXOCONCHA* Sars, 1866

Remarks. The four species described here differ ornamentally by having either a reticulate or a pitted shell surface. We have grouped the species according to this and, as will be discussed under environment, we show that this has a bearing on their distribution either within the lagoon or outside on the nearshore shelf.

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Reticulate species

Loxoconcha (Loxoconcha) multiornata sp. nov.
(Figs 1A–J, 2 & 11)

Loxoconcha ornatovalvae Hartmann; Bate 1971 : 245, 246, 248, 250, pl. 1, figs. 1k & 2k, pl. 2, fig. 3k, pl. 3, figs. 2k & 3k.
Loxoconcha sp. A, Jain 1978 : 126, fig. 5A.

HOLOTYPE. BM(NH) no. 1980.236, ♂ carapace, sample 6514, central lagoon terrace.

PARATYPES. BM(NH) nos 1980.237–243.

TYPE LOCALITY. Sample 6514—Central lagoon terrace, shallow marine, tidal; salinity 50·75‰.

DIAGNOSIS. Species of *Loxoconcha* having very coarsely reticulate ornamentation (as illustrated) with some reticulae developed into ridges; dorsal ridge of carapace characteristically producing pear-shaped pattern.

DESCRIPTION. Species dimorphic, the males more elongate than the females. Ornamentally the reticulae are very coarsely developed and may even be produced as low ridges. The eye node is developed as a swelling situated on a low antero-dorsal ridge. Sieve plate normal pores are situated within the reticulae. Ventrally, the edge of the right valve, where it overlaps the left, is marked with short ridges while the left valve in the posterior part of the carapace possesses four rowlock-type projections (Fig. 1D). Hinge typically gongylodont with coarsely dentate/loculate median element. Muscle scars with three oval adductor scars in a vertical row with a fourth situated almost in front of the lowermost scar. Frontal scar V-shaped. Duplicature broad with small antero-ventral and narrow postero-ventral vestibule. Marginal canals straight, widely spaced and few in number: 9 anteriorly. Outside the selvage a broad flange extends around the anterior and along the ventral margin.

DIMENSIONS. Holotype: 1980.236 ♂ carapace, length 0·46 mm; height 0·26 mm; width 0·26 mm. Paratypes: 1980.237 ♂ RV., length 0·47 mm; height 0·26 mm. 1980.238 ♀ carapace, length 0·38 mm; height 0·24 mm; width 0·23 mm. 1980.239 ♀ carapace, length 0·40 mm; height 0·25 mm; width 0·23 mm. 1980.240 ♂ carapace, length 0·50 mm; height 0·26 mm; width 0·28 mm. 1980.241 ♀ RV., length 0·40 mm; height 0·24 mm. 1980.242 ♂ RV., length 0·44 mm; height 0·25 mm.

REMARKS. *Loxoconcha (Loxoconcha) multiornata* sp. nov. is morphologically very close to the Red Sea species, *Loxoconcha ornatovalvae* Hartmann 1964 and was, in fact, identified as such by one of us (Bate, 1971). There are, however, significant differences that make separation of the two species possible: firstly in dorsal view, the curved dorsal ridge of *L. multiornata* produces a pear-shaped pattern when both valves are together (Fig. 1E, F) whereas in *L. ornatovalvae* (Hartmann, 1964, pl. 20, fig. 93) there is a looped ridge pattern extending from the eye node back along the dorsal margin. The eye node of the Red Sea species is separate from the antero-dorsal ridge, whereas in *L. multiornata* it is a swollen part of the ridge. The differences in the lateral ornamentation are best explained by illustration (see Fig. 2).

Loxoconcha (L.) multiornata has been recorded by Jain 1978 as *Loxoconcha* sp. A from the Recent sediments of Mandvi Beach, west coast of India and is thus known to occur within the Indian Ocean area. As yet it has not been recorded from the African coast. If, as appears possible, the Red Sea *Loxoconcha ornatovalvae* has developed from the Indian Ocean/Persian Gulf *L. multiornata*, then we are going some way to implying that species give rise to similarly ornamented species and this could lead us to a subdivision of the subgenus *Loxoconcha* on basic external morphology. By grouping the five species described in this paper on similar ornamentation we are partly suggesting this but we would not claim that the groupings here necessarily relate to all the species described here.

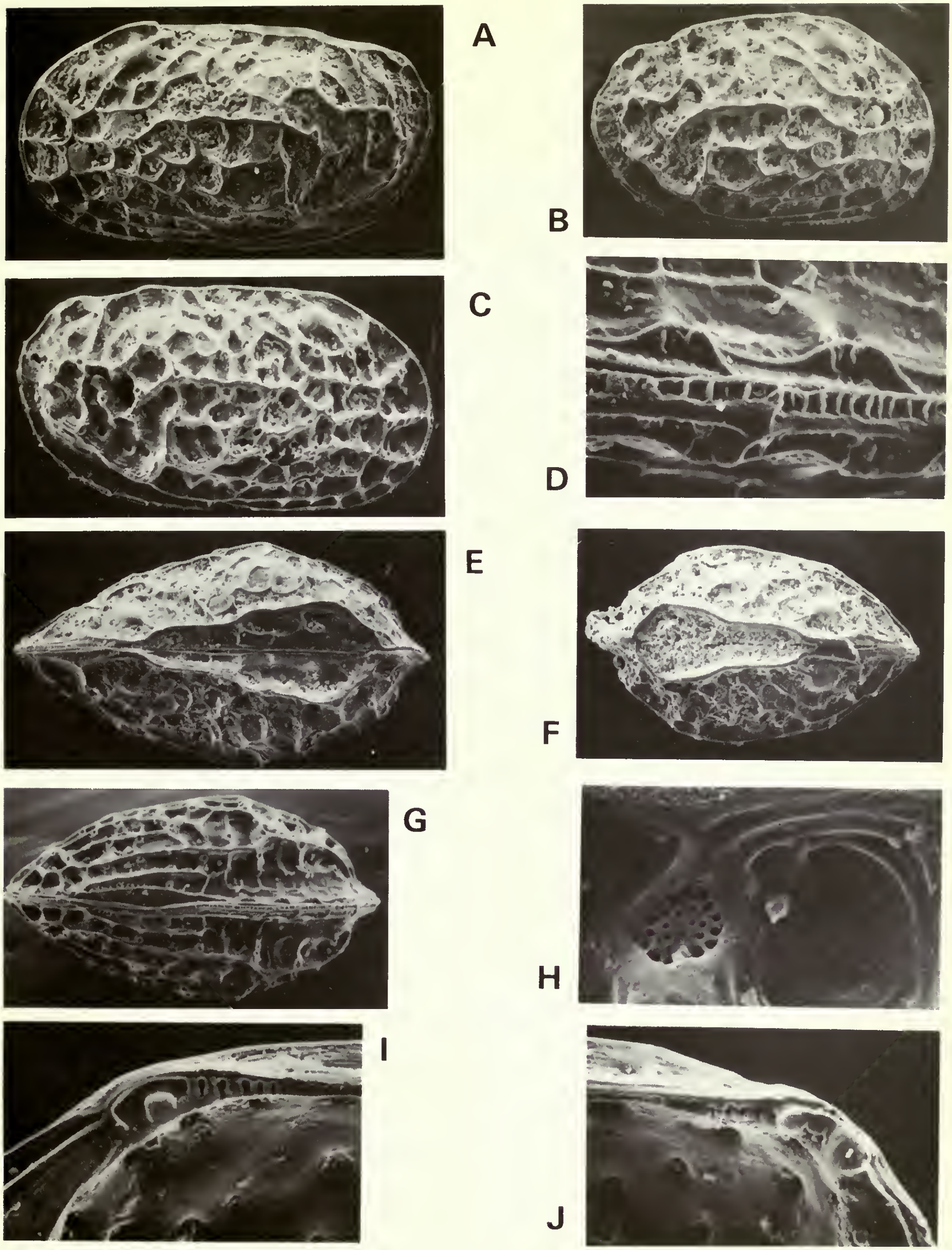

Fig. 1 *Loxoconcha (Loxoconcha) multiornata* sp. nov.: A, X 125, holotype, ♂ left side, BM(NH) 1980.236; B, X 125, paratype ♀ RV., specimen lost; C, X 125, paratype ♂ RV., BM(NH) 1980.237; D, G, enlargement of ventral margin X 580 and ventral view of carapace X 125, ♀ paratype BM(NH) 1980.239; H, X 1·12K, sieve plate, specimen lost; E, X 125, paratype ♂ dorsal carapace, BM(NH) 1980.240; F, X 125, paratype ♀ dorsal carapace, BM(NH) 1980.239; I, J, X 345, paratype ♀ terminal hinge elements RV, BM(NH) 1980.241.

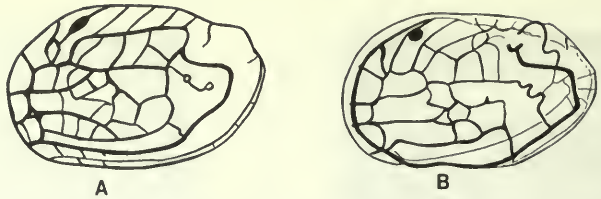

Fig. 2 Comparison of ornamentation between *Loxoconcha (Loxoconcha) multiornata* sp. nov. [A] and *Loxoconcha (Loxoconcha) ornatovalvae* Hartmann [B].

DISTRIBUTION. *Loxoconcha (L.) multiornata* is essentially a nearshore shelf species but does occur sporadically in the inner, central and outer lagoon areas (Fig. 11).

Loxoconcha (Loxoconcha) gurneyi sp. nov.
(Figs 3A–K, 4 & 11)

Loxoconcha sp. A. (pars), Bate 1971 : 245, 246, 248, pl. 1, figs 11, 21, pl. 2, figs 21, 31 & pl. 3, figs 11, 21 & 31.

Loxoconcha sp. B., Jain 1978 : 126, fig. 5B.

DERIVATION OF NAME. Named in honour of Dr Robert Gurney, 1879–1950, Zoologist, well known for his work on Crustacea.

HOLOTYPE. BM(NH) no. 1980.245, ♂ LV. sample 62107, nearshore shelf.

PARATYPES. BM(NH) nos 198.246–251 & 431.

TYPE LOCALITY. Sample 62107, nearshore shelf; shallow marine; salinity 43·75‰; surface water temperature 23·0–24·4°C.

DIAGNOSIS. Species of *Loxoconcha* with neat, honeycomb reticulation.

DESCRIPTION. Carapace quadrate (♀) to rectangular (♂) with straight dorsal margin; sinuous ventral margin; broadly rounded anterior and posteroventral margins; posterodorsal margin short and concave. Eye node oval, situated below anterior cardinal angle. Entire shell surface covered by neat reticulation of somewhat rounded, 5-sided, pits; the pits becoming 4-sided around the posterior margin and along the dorsal and ventral surfaces. Ventral margin of right valve ornamented by short ridges situated perpendicular to valve edge (Fig. 3B). Normal pore canals open, through a sieve plate, on the murae of the reticulation. Hinge, well developed gongylodont. Muscle scars with a vertical row of 4 adductors and an oval frontal scar (Fig. 3G). Duplicature broad around anterior (with a narrow vestibule) and in the posteroventral region; eight long, straight and widely spaced anterior canals. A distinct flange extends around the entire free margin. Copulatory appendage with small, blunt-ended, lappet (Fig. 4).

DIMENSIONS. Holotype: 1980.245, ♀ carapace, length 0·50 mm; height 0·29 mm; width 0·27 mm. Paratypes: 1980.246, ♂ LV., length 0·53 mm; height 0·28 mm. 1980.247, ♂ RV., length 0·52 mm; height 0·28 mm. 1980.248, ♂ RV., length 0·49 mm; height 0·27 mm. 1980.249, ♀ carapace, length 0·49 mm; height 0·31 mm; width 0·25 mm. 1980.250, ♂ LV., length 0·53 mm; height 0·29 mm.

REMARKS. *Loxoconcha (L.) gurneyi* sp. nov. has previously been figured as *Loxoconcha* sp. A. by Bate from the Persian Gulf and as *Loxoconcha* sp. B. by Jain from Mandvi Beach, west coast of India. *Loxoconcha gruendeli* Jain 1978 from Mandvi beach is very close to this species but differs by having pits rather than reticulae in the dorsal region and by having a smooth posterior border; in *L. (L.) gurneyi* short ridges cross the posterior border. Like *L. (L.) multiornata,* a series of short ridges occur along the free outer margin of the ventral edge of the right valve (Fig. 3B, D). A number of individual valves completely lack a duplicature

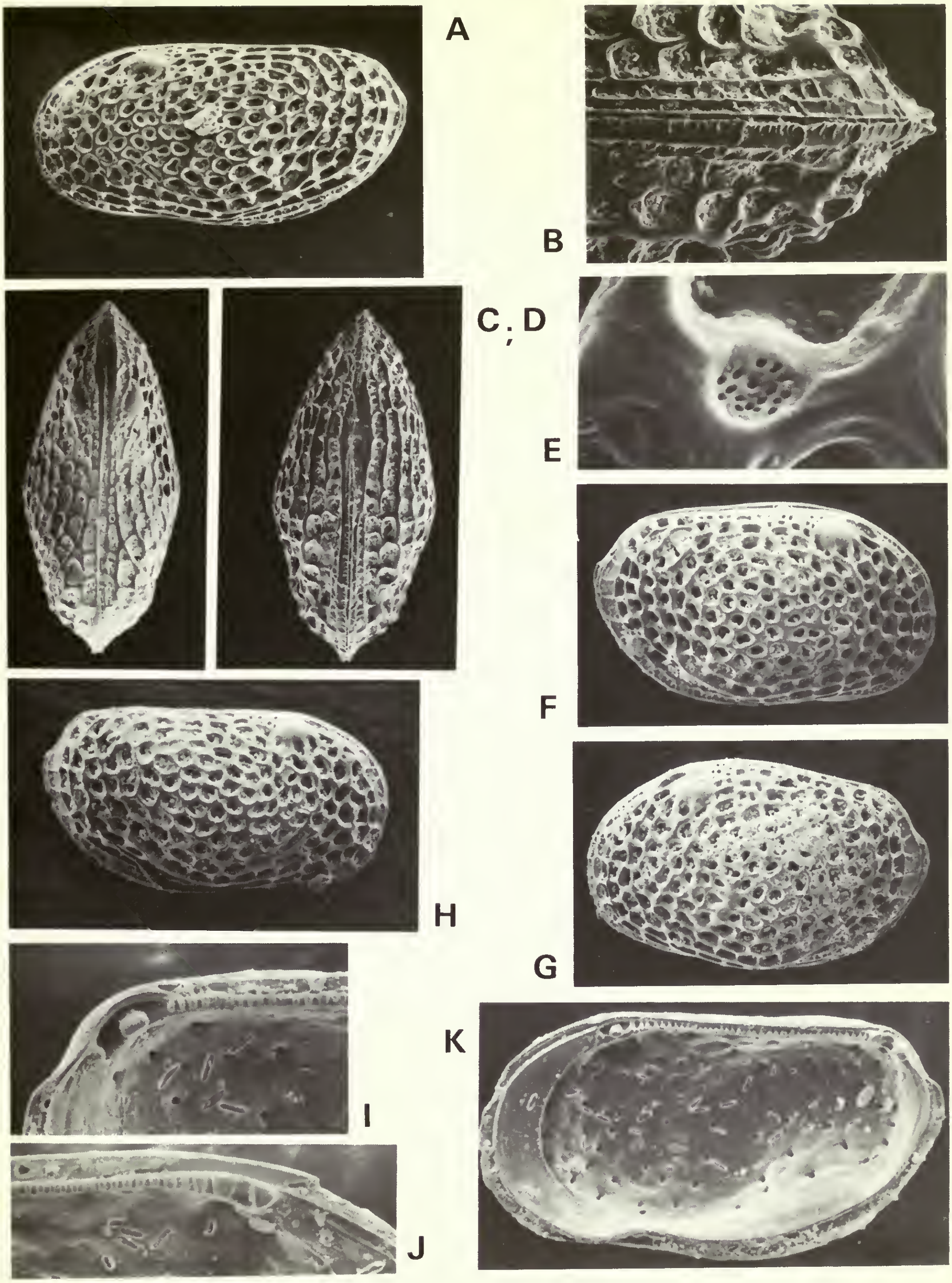

Fig. 3 *Loxoconcha (Loxoconcha) gurneyi* sp. nov.: A, E, LV. X 100 and sieve plate X 600, ♂ holotype BM(NH) 1980.250; B, D, enlarged view posteroventral margin X 200 and ventral surface X 100 ♂ carapace, specimen lost; C, X 100, paratype ♂ dorsal carapace, specimen lost; F, X 100, paratype ♀ left carapace, BM(NH) 1980.249; G, X 100, holotype ♀ right carapace, BM(NH) 1980.245; H, X 100, paratype ♂ RV., BM(NH) 1980.248; I, J, X 250, paratype ♂ terminal hinge elements RV., BM(NH) 1980.246; K, X 125, paratype ♂ internal RV., BM(NH) 1980.247.

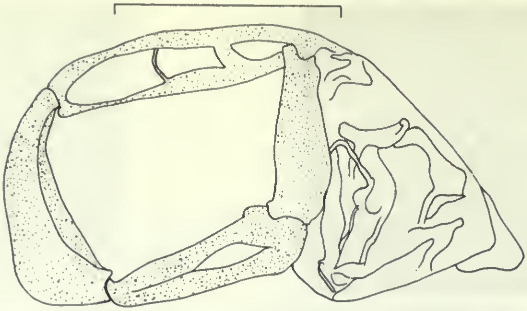

Fig. 4 Copulatory appendage of *Loxoconcha (Loxoconcha) gurneyi* sp. nov. ♂ paratype BM(NH) 1980.431. Scale bar represents 0·1 mm.

(e.g. BM(NH) no. 1980.250)—this is considered to be due to the animal dying immediately after moulting and before calcification of the duplicature part of the inner lamella.

DISTRIBUTION. *Loxoconcha (L.) gurneyi* sp. nov. is a nearshore shelf species in the Persian Gulf—its presence in Abu Dhabi lagoon (Fig. 11) was almost certainly the result of being taken into the lagoon by tidal currents.

Pitted species

Loxoconcha (Loxoconcha) indica Jain, 1978
(Figs 5A–H & 11)

Loxoconcha sp. C., Bate 1971 : 246, 250, pl. 3, figs. 2n, 3n.
Loxoconcha megapora indica n. subsp. Jain 1978 : 126, figs. 4L 1–2; 6P.

TYPE LOCALITY. Mandvi beach, west coast of India.

DIAGNOSIS (emended). Small species of *Loxoconcha* having densely pitted surface ornamentation. Posteroventral margin of carapace broadly convex; posterior end broadly rounded with short, weakly concave, posterodorsal margin. Carapace convex in dorsal view; eye nodes distinct.

DESCRIPTION. Carapace dimorphic, males rectangular, females quadrate; both sexes with broadly rounded anterior and posterior ends, posterodorsal margin being short and insignificantly concave. Eye node distinct. Shell surface covered by a dense, finely pitted ornamentation, smooth patches medianly and dorsally marking the location of muscles on the inside of the shell. Periphery of carapace with very fine network of striae. Normal pores open to exterior by means of a sieve plate. Left valve larger than right. Hinge gongylodont, muscle scars a subvertical row of 4 oval scars with a crescent-shaped anterodorsal frontal scar and two, large, rounded, anteroventral mandibular scars. Duplicature of moderate width with a distinct vestibule extending around the anterior end; anterior marginal canals long, straight and widely spaced; approximately 9–10 anteriorly.

DIMENSIONS. 1980.252, ♂ carapace, length 0·49 mm; height 0·26 mm; width 0·23 mm. 1980.253, ♀ LV., length 0·42 mm; height 0·26 mm. 1980.254, ♂ carapace, length 0·48 mm; height 0·26 mm; width 0·23 mm. 1980.255, ♀ RV., length 0·41 mm; height 0·26 mm. 1980.256, ♀ carapace, length 0·43 mm; height 0·27 mm; width 0·22 mm.

REMARKS. *Loxoconcha (L.) indica* Jain, 1978 was first described as a subspecies of *L. megapora* Benson & Maddocks, 1964 by Jain from Mandvi beach, west coast of India. *L. megapora*, a smooth species found in the Knysna estuary, South Africa has a different dorsal outline (being parallel-sided to slightly concave) to Jain's material and the two are not considered to be conspecific. Jain's subspecies is, therefore, raised to specific status.

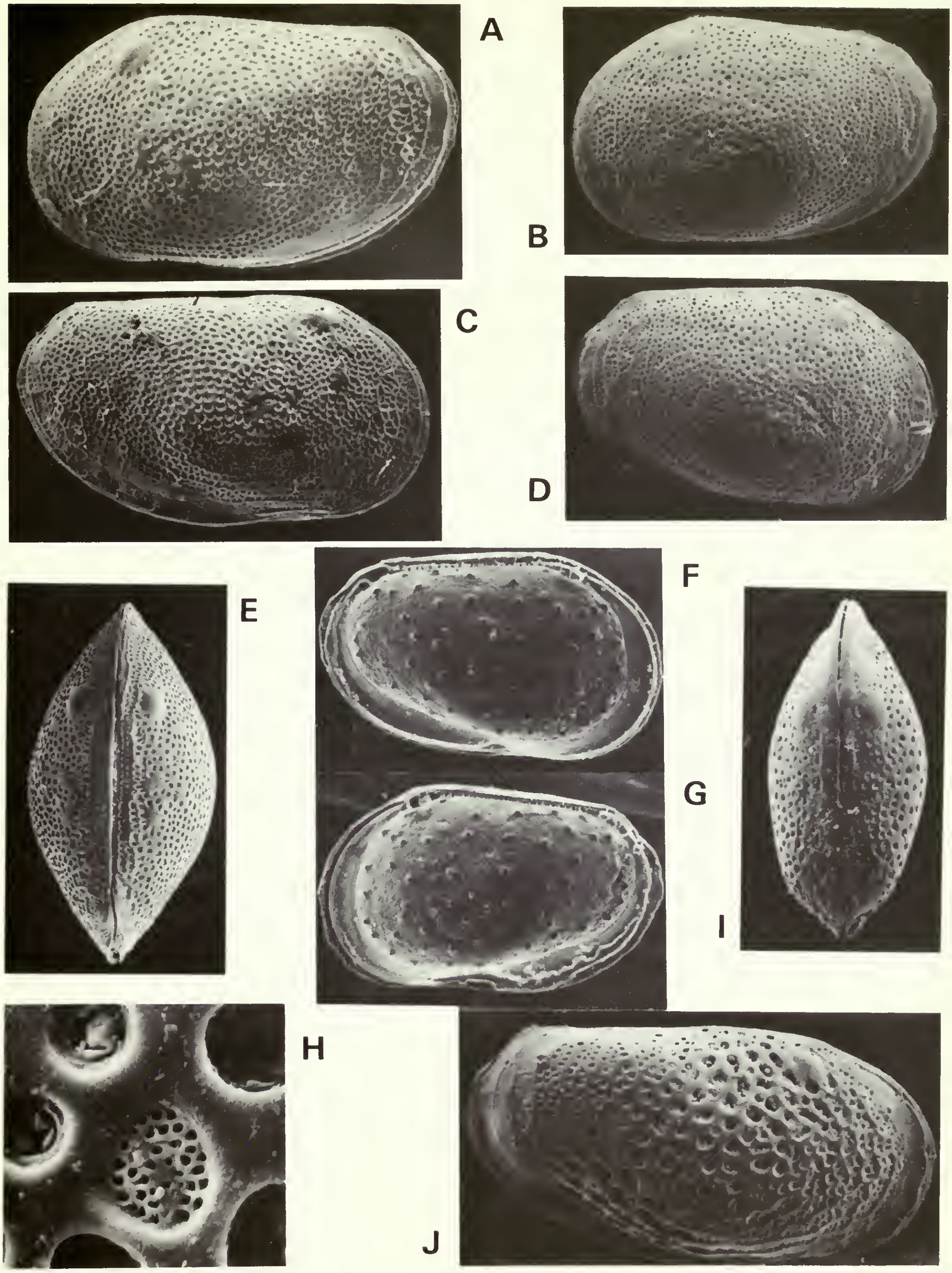

Fig. 5 *Loxoconcha (Loxoconcha) indica* Jain. A, H, ♂ left carapace X 125 and sieve plate X 750, BM(NH) 1980.252; B, F, ♀ LV. X 125 and internal view X 100, BM(NH) 1980.253; C, X 125, ♂ right carapace, BM(NH) 1980.254; D, G, external view X 125 and internal view, X 100, ♀ RV. BM(NH) 1980.255; E, X 125, dorsal view, ♀ carapace BM(NH) 1980.256. *Loxoconcha (Loxoconcha) amygdalanux* sp. nov. I, X 125, paratype dorsal carapace –2 instar, BM(NH) 1980.257; J, X 118, holotype ♂ RV. BM(NH) 1980.258.

Loxoconcha sp. C. recorded by Bate, 1971 from Abu Dhabi lagoon, Persian Gulf is considered to be conspecific with Jain's *L. indica* even though the postero-ventral margin of the Persian Gulf material is more broadly convex; the geographical range of the species is thus extended. Laterally *L. indica* has a superficial resemblance to *L. matagordensis* Swain, 1955 from San Antonio Bay, Texas but lacks the posterodorsal *Loxocorniculum* projection, anterior marginal ridges and oblique anterodorsal slope of *matagordensis.* Ornamentally, there are many species, including *L. rhomboidea*—the type species, that possess the type of ornamentation exhibited here; carapace outline differences as well as the male copulatory appendage being used to distinguish between them. Unfortunately although females with appendages occur for *L. indica* no male was available for dissection. *Loxoconcha* spec. illustrated by Hartmann (1980, pl. 10, figs. 14, 15) from Pt. Welshpool, Australia is comparable in shape with *L. indica* although lacking the straight dorsal margin of the latter and having a much more finely pitted ornamentation.

DISTRIBUTION. Mandvi Beach, west coast India and in the Persian Gulf where it occurs on the shallow terraces of Abu Dhabi lagoon having a salinity tolerance of 44·80–55·30‰ and a surface water temperature of 20–36·2°C; so far only found allochthonously on the nearshore shelf.

Loxoconcha (Loxoconcha) amygdalanux sp. nov.
(Figs 5, I, J; 6, A–K; 7; 8, A–C & 11)

Loxoconcha sp. B., Bate 1971 : 245, 246, 248, pl. 1, fig. 2 m; pl. 2, fig. 3 m.
Loxoconcha sp. A., Paik 1977 : 56, 58, pl. 6, figs. 112–114.

DERIVATION OF NAME. Latin *amygdala*, almond + *nux*, a nut.

HOLOTYPE. BM(NH) no. 1980.258, ♂ RV., sample 6278, back reef, nearshore shelf.

PARATYPES. BM(NH) nos 1980.257 & 259–263, 269 & 430.

TYPE LOCALITY. Sample 6278 nearshore reef; salinity gradient 43·05–44·45‰; surface temperature 23·0–33·6°C.

DIAGNOSIS. Coarsely pitted species of *Loxoconcha* in which pits are larger towards centre of valve. Dimorphism distinct: females subquadrate, males rectangular. Posteroventral border broadly convex in female, less so in male. Male with distinct postero-ventrolateral carapace indentation. Copulatory appendage shovel-shaped with small, triangular, terminally pointed lappets.

DESCRIPTION. Carapace quadrate with broadly rounded anterior margin and deep, convex posteroventral margin and straight to slightly convex dorsal margin in the female. Male very elongate with rounded anterior and deep depression in posterior ventrolateral surface. Eye nodes in both dimorphs distinct. Ornamentation of large pits more evenly sized in the female. In the male the pits are very much larger towards the centre of each valve. Normal pore sieve plates situated on broad murae between pits. Left valve only slightly larger than right, almost equivalve. In ventral view female carapace has appearance of an almond, from which the species name has been taken. Internally the hinge is well developed, gongylodont. Muscle scars a curved row of four adductors, an anterocentral crescent-shaped frontal scar and two oval anteroventral mandibular scars. Duplicature broad with narrow anterior and posteroventral vestibules. 9 anterior marginal canals, long, straight and widely spaced. Copulatory appendage shovel-shaped with small, triangular, terminally pointed lappets.

DIMENSIONS. Holotype: 1980.258, ♂ RV., length 0·57 mm; height 0·30 mm. Paratypes: 1980.257, –2 instar, carapace, length 0·38 mm; height 0·22 mm; width 0·19 mm. 1980.259, ♂ LV., length 0·58 mm; height 0·29 mm. 1980.260, –2 instar, carapace, length 0·40 mm; height 0·26 mm; width 0·22 mm. 1980.261, –2 instar, LV., length 0·34 mm; height 0·19 mm. 1980.262, ♀ RV., length 0·49 mm; height 0·30 mm. 1980.263, ♀ RV., length 0·43 mm; height

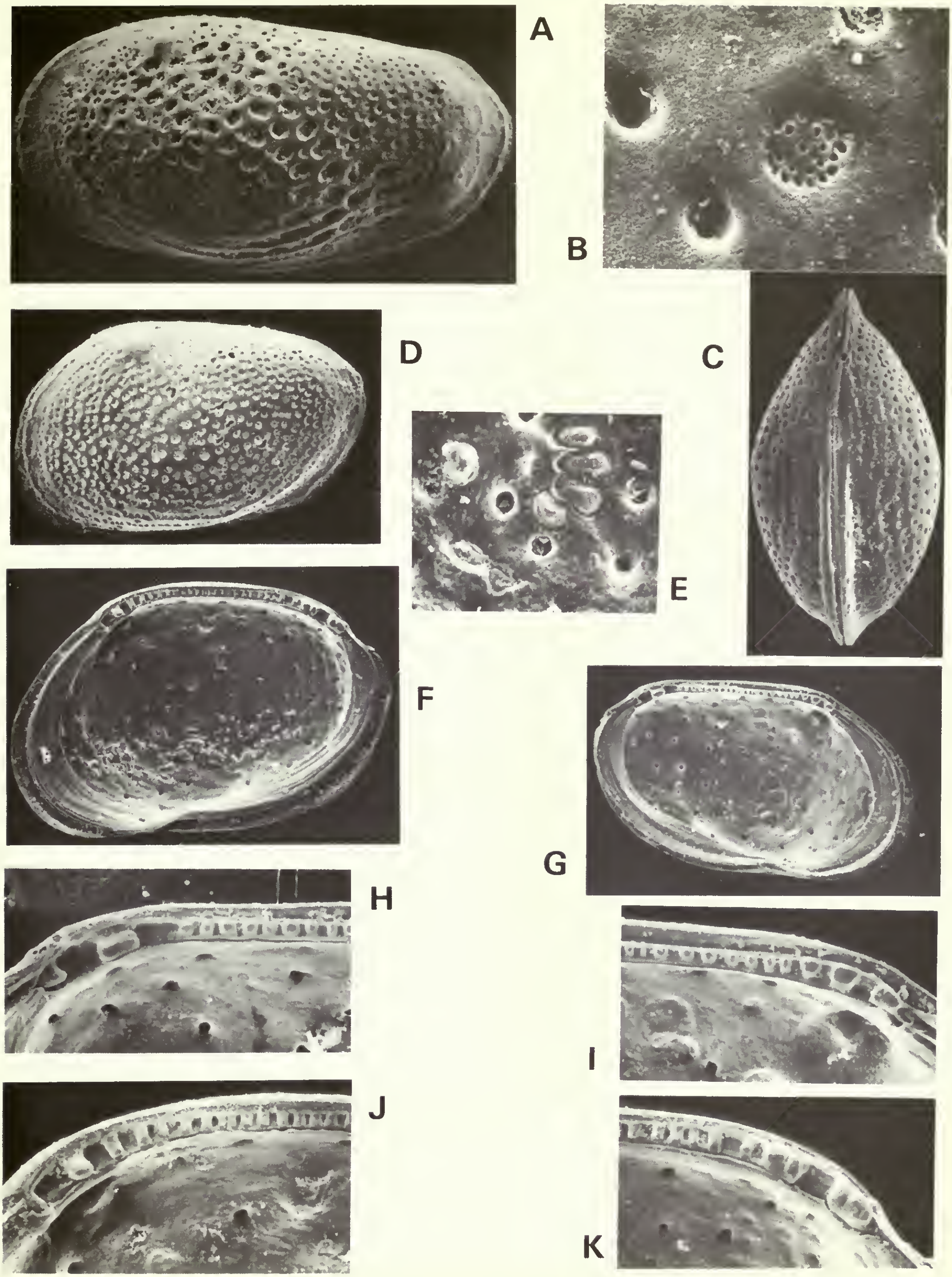

Fig. 6 *Loxoconcha (Loxoconcha) amygdalanux* sp. nov.: A, X 122, paratype ♂ LV., BM(NH) 1980.259; B, D, sieve plate X 1·05K and external view X 125 –2 instar LV, paratype BM(NH) 1980.261; C, X 127, paratype ventral carapace –2 instar, BM(NH) 1980.260; E, X 260 muscle scars paratype ♀ RV, BM(NH) 1980.262; F, J, K, internal view X 123 and terminal hinge elements X 265, female RV., paratype BM(NH) 1980.263; G, H, I, internal view X 122 and terminal hinge elements X 350, –2 instar LV., paratype BM(NH) 1980.264.

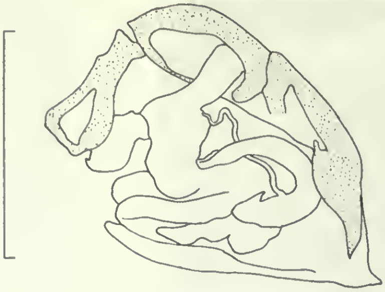

Fig. 7 Copulatory appendage of *Loxoconcha (Loxoconcha) amygdalanux* sp. nov. ♂ paratype, BM(NH) 1980.430. Scale bar represents 0·1 mm.

0·27 mm. 1980.264, –2 instar, LV., length 0·40 mm; height 0·22 mm. 1980.265, –2 instar, RV., length 0·38 mm; height 0·22 mm. 1980.266, –1 instar, RV., length 0·41 mm; height 0·26 mm. 1980.267, –2 instar, LV., length 0·37 mm; height 0·24 mm.

REMARKS. *Loxoconcha (L.) amygdalanux* sp. nov. has been recorded from the Gulf of Oman and the Persian Gulf by Paik (1977) who records this species from his faunal zones A to C, open marine conditions ranging in depth from 7 to 208 metres. The coarse ornamentation, particularly towards the centre of the carapace, in association with carapace outline clearly sets this species apart from all others described from the Gulf/Indian Ocean region. Neither has any comparable species been described by Hartmann from the Red Sea nor Australia.

DISTRIBUTION. Nearshore shelf and outer lagoon channels, Abu Dhabi lagoon; Central Basin Persian Gulf and Biaban Shelf, Gulf of Oman.

Subgenus ***EPAKROCONCHA*** nov.

DERIVATION OF NAME. Greek *epakros*, pointed at the end + *concha*, Latin, shell.

GENDER. Feminine.

TYPE SPECIES. *Epakroconcha batei* sp. nov.

DIAGNOSIS. Carapace subtrigonal in lateral outline of both dimorphs with left valve dorsal margin umbonate; right valve dorsal margin almost straight. Left valve larger than right. Eye node distinct. Normal pore canals with sieve plate. Shell surface ornamented. Hinge gongylodont. Muscle scars with 4 oval adductors, a crescent-shaped frontal and an oval anteroventral mandibular. Anterior and posteroventral duplicature broad with vestibula and straight marginal canals, few in number. First antenna long, slender, 6 jointed with 4 terminal bristles. 2nd antenna with two terminal claws and long spinneret bristle. Maxilla with small comb of spines on inner (1st) endite and having approx. 16 (one aberrant) bristles on respiratory plate. Walking legs slender. Copulatory appendage boot-shaped with small terminally rounded lappet.

REMARKS. *Epakroconcha* subgen. nov. differs from other loxoconchid genera by having a subtrigonal shell outline in both dimorphs; the male being only slightly more elongate than the female.

Loxoconcha (Epakroconcha) batei sp. nov.

(Figs 8, D–H; 9, A–C; 10 & 11)

DERIVATION OF NAME. Named in honour of Charles Spence Bate 1818–1889 for his work on Recent crustacea.

HOLOTYPE. BM(NH) no. 1980.271, ♂ carapace, sample 1094, central lagoon terrace.

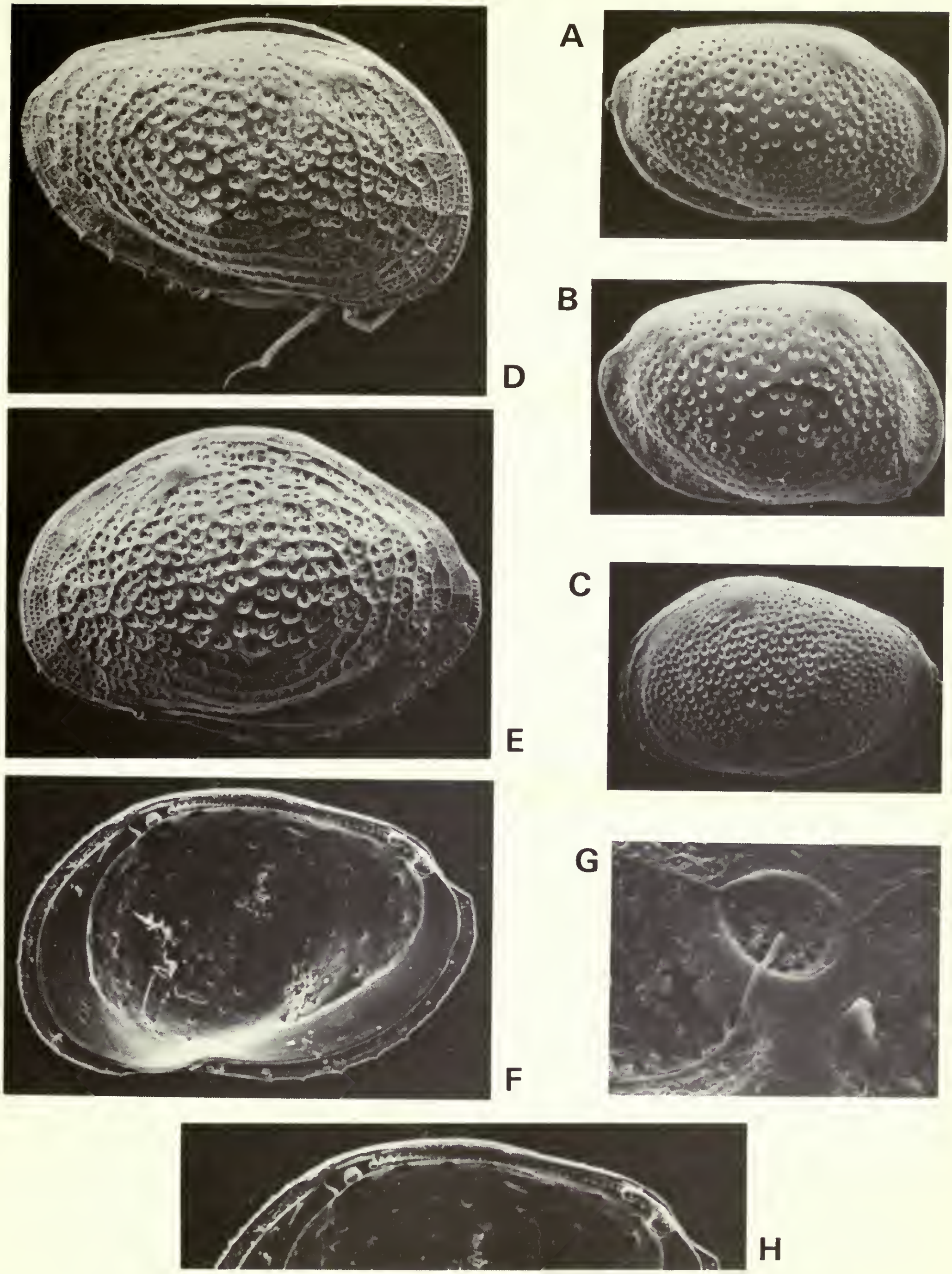

Fig. 8 *Loxoconcha (Loxoconcha) amygdalanux* sp. nov.: A, X 126, RV., –2 instar, paratype BM(NH) 1980.265; B, X 118, RV., –1 instar, paratype BM(NH) 1980.266; C, X 122, LV., –2 instar, paratype BM(NH) 1980.267. *Loxoconcha (Epakroconcha) batei* subgen. et sp. nov.: D, X 124, paratype ♂ right carapace, BM(NH) 1980.268; E, X 137, paratype ♀ left carapace, BM(NH) 1980.269; F, H, internal view X 132 and hinge X 146, ♀ RV., paratype BM(NH) 1980.270; G, X 2K, holotype ♂, sieve plate, BM(NH) 1980.271.

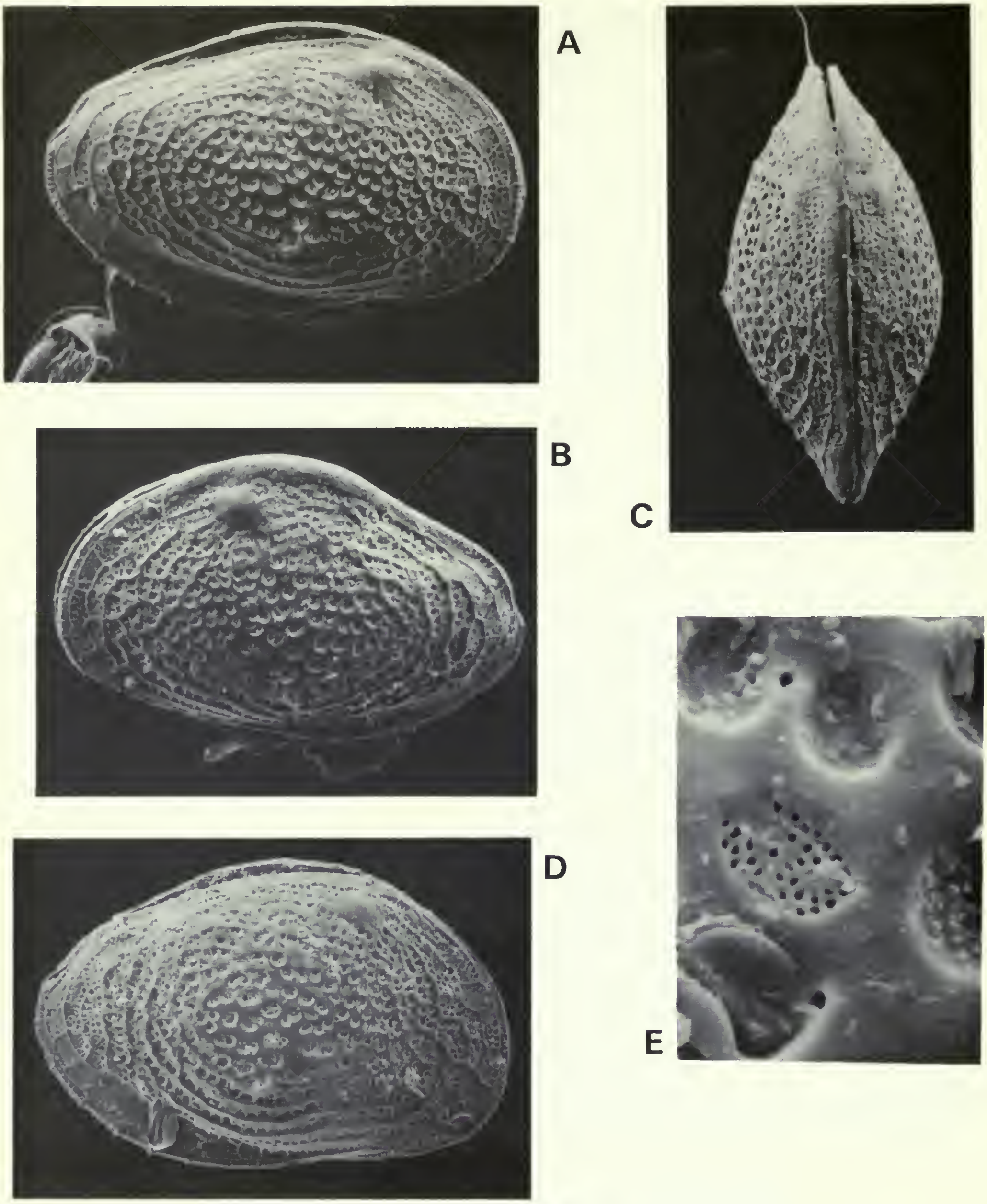

Fig. 9 *Loxoconcha (Epakroconcha) batei* subgen. et sp. nov.: A, X 127, holotype ♂ right carapace, BM(NH) 1980.271; B, X 121, paratype ♂ left carapace, BM(NH) 1980.272; C, X 122, paratype ♀ dorsal carapace, BM(NH) 1980.273. D, X 125, paratype ♀ right carapace, BM(NH) 1980.428. E, X 1·8K, sieve plate, paratype ♀ right carapace, BM(NH) 1980.428.

Fig. 10 *Loxoconcha (Epakroconcha) batei* subgen. et sp. nov. Appendages and copulatory organ. Scale A—0·1 mm for appendages; scale B—0·1 mm for copulatory organ. A, F, 1st antenna and copulatory organ, ♂ paratype, BM(NH) 1980.433; B, C, D, 2nd antenna, mandible and maxilla, ♀ paratype, BM(NH) 1980.432; E, 1st, 2nd & 3rd thoracic appendages, ♀ paratype, BM(NH) 1980.429.

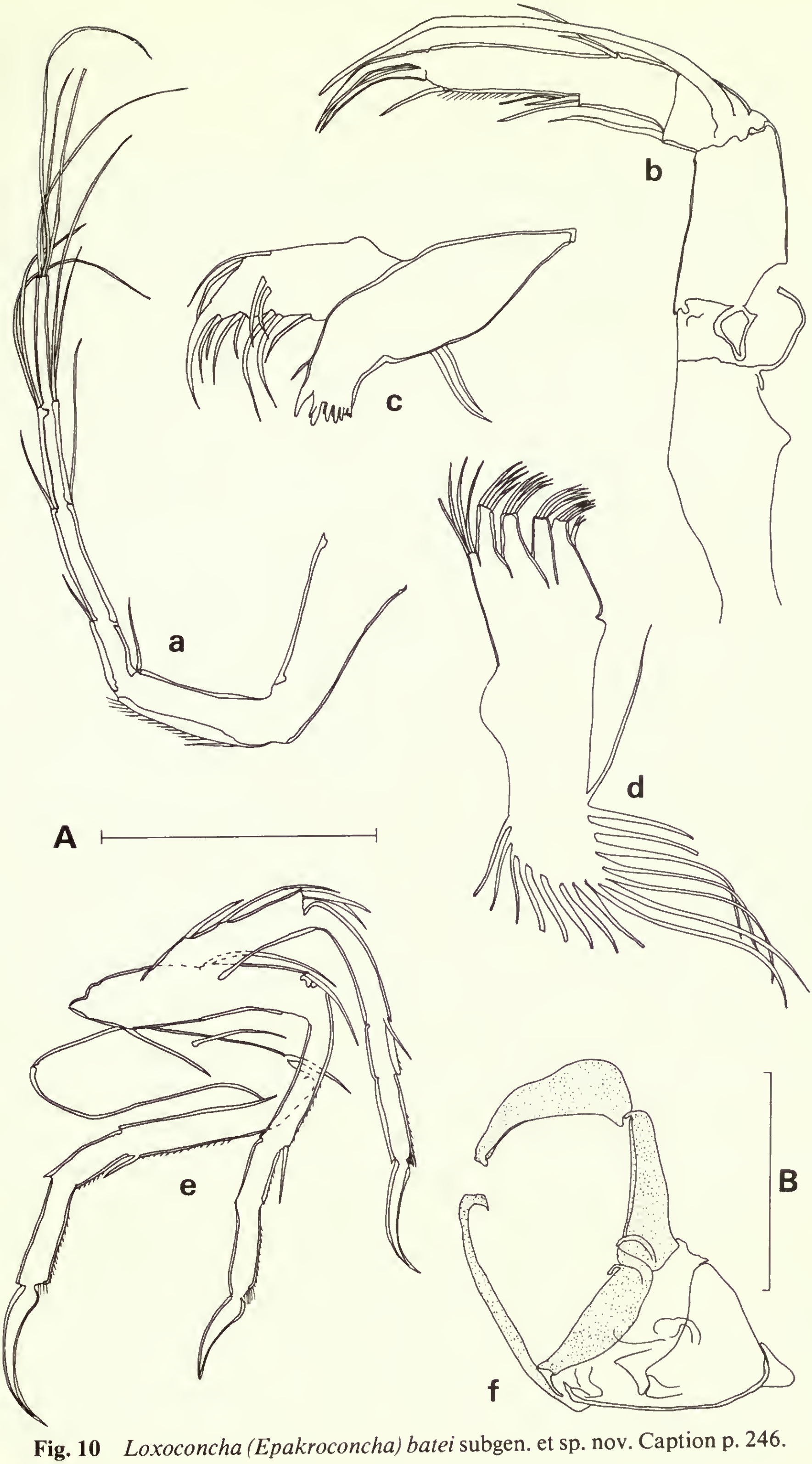

Fig. 10 *Loxoconcha (Epakroconcha) batei* subgen. et sp. nov. Caption p. 246.

PARATYPES. BM(NH) nos 1980.268–270, 272–273, 428–9 & 432–3.

TYPE LOCALITY. Sample 1094, weed sample preserved in alcohol, inner lagoon terrace. Shallow water marine, tidal; salinity gradient 49·70–55·3‰; surface temperature of 20·5–36·2°C.

DIAGNOSIS. Species of *Epakroconcha* having coarsely pitted shell ornamentation, the pits larger towards centre of each valve. Periphery of carapace with fine network of striae. Posteroventral border of right valve with five small marginal denticles; denticles smaller and sometimes fewer in left valve. Small tubercle present on ventrolateral part of shell just below mid point, more clearly seen in dorsal or ventral view. Approximately 8 straight anterior marginal canals; 3 posterior canals. Copulatory appendage boot-shaped with small rounded-triangular lappet.

DESCRIPTION. Carapace subtrigonal in lateral outline; dorsal margin umbonate in the left valve. Anterior margin of both valves rounded; posterior with deep, convex posteroventral margin and short concave, posterodorsal margin. Left valve over-reaches right along dorsal margin. Males slightly more elongate than females. Eye node distinct; shell surface coarsely ornamented with large pits that decrease in size towards valve margins in which region a reticulation of low ridges (peripherally striae) are superimposed. A low tubercle is developed below mid-point on each valve, more clearly observed in dorsal or ventral view. Posteroventral margin with five, small, marginal denticles. Normal pores with slightly recessed sieve plate each bearing a central setal pore: setae long and slender. Hinge gongylodont. Muscle scars with an oval to crescent-shaped frontal scar situated medially in front of 4 oval adductor scars, mandibular scar elongate-oval, situated well below adductors. Duplicature broad, with broad anterior and posterior vestibula; marginal canals short, straight, approximately 8 anteriorly, 3 posteriorly and 6 posteroventrally. 1st antenna long, slender, 6 jointed with 4 slender terminal bristles and 4 bristles at distal end of penultimate podomere. 2nd antenna with two strong terminal claws and long spinneret bristle; terminal two podomeres fused. Mandible with strong masticatory process. Maxilla with blade-like respiratory process having 16 bristles (or less) of which one is aberrant. Thoracic limbs slender with strong terminal claws. Copulatory appendage boot-shaped with small, terminally rounded lappet.

DIMENSIONS. Holotype: 1980.271 ♂ carapace, length 0·52 mm; height 0·32 mm; width 0·23 mm. Paratypes: 1980.268 ♂ carapace, length 0·51 mm; height 0·31 mm; width 0·24 mm. 1980.269, ♀ carapace, length 0·49 mm; height 0·34 mm; width 0·25 mm. 1980.270, ♀ RV., length 0·50 mm; height 0·32 mm. 1980.272 ♂ carapace, length 0·52 mm; height 0·31 mm; width 0·26 mm. 1980.273 ♀ carapace, length 0·50 mm; height 0·33 mm; width 0·26 mm. 1980.428 ♀ carapace, length 0·52 mm; height 0·35 mm; width 0·25 mm. 1980.429 ♀ RV., length 0·49 mm; height 0·29 mm.

REMARKS. *Loxoconcha (Epakroconcha) batei* sp. nov. is readily separable from previously described species of the genus on its subtrigonal lateral outline and spinose posteroventral margin.

DISTRIBUTION. Inner lagoon and lagoon channels, Abu Dhabi lagoon. Transported as dead valves onto the nearshore shelf.

Environment

It is popularly regarded that the strength of the carapace ornamentation of an ostracod is a direct reflection on the nature of the environment in which the species lives. A coarse ornament reflects an adaptation to survival within a high energy environment and a poorly ornamented shell is suitable for quieter low energy environments. This does not necessarily hold true for burrowing forms nor for those that are able to shelter within dense patches of weed or among growing coral communities. Also many genera are totally smooth for all their

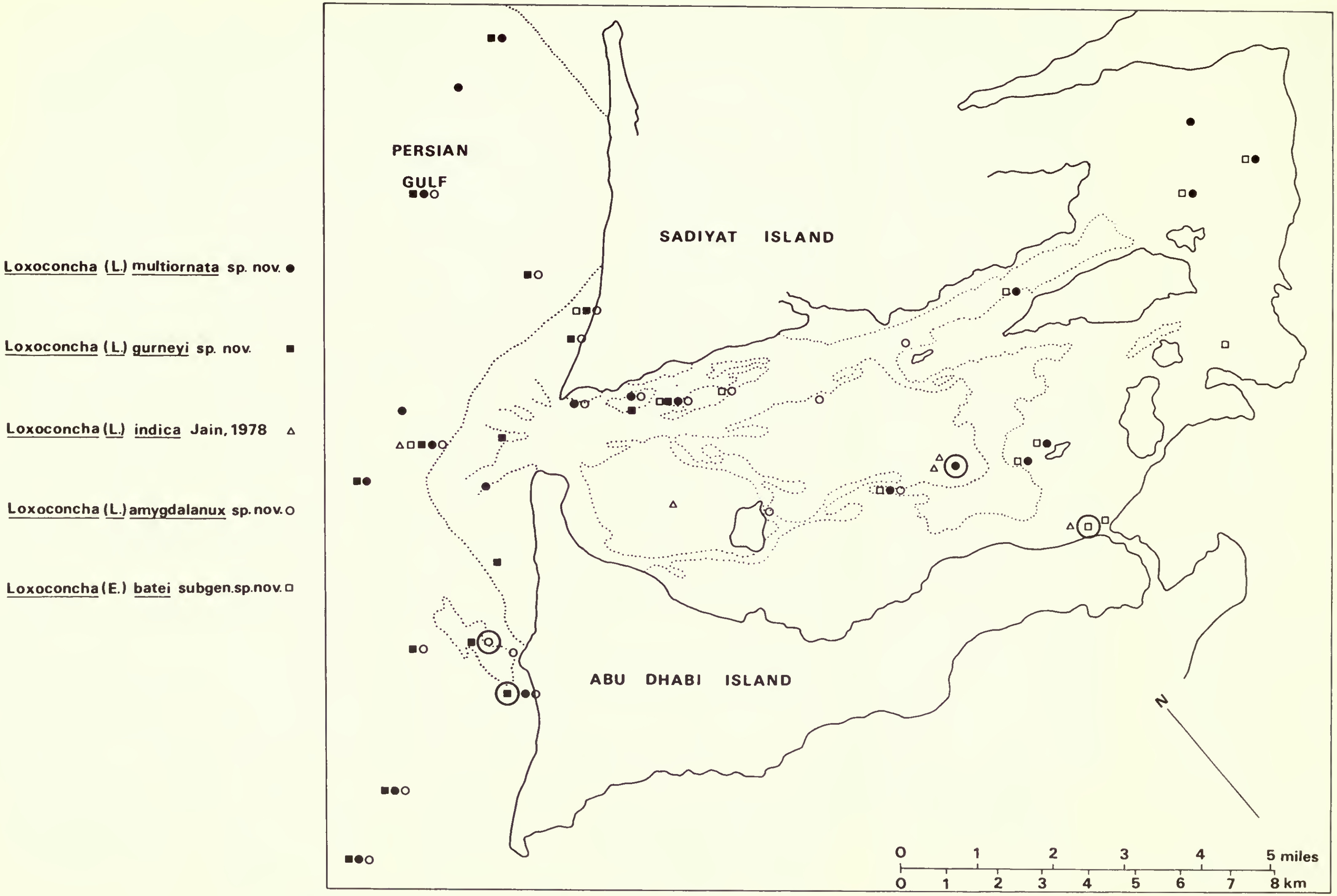
PERSIAN
GULF
SADIYAT ISLAND
ABU DHABI ISLAND
N
0 1 2 3 4 5 miles
0 1 2 3 4 5 6 7 8 km
Loxoconcha (L.) multiornata sp. nov. ●
Loxoconcha (L.) gurneyi sp. nov. ■
Loxoconcha (L.) indica Jain, 1978 △
Loxoconcha (L.) amygdalanux sp. nov. ○
Loxoconcha (E.) batei subgen. sp. nov. □

Fig. 11 Distribution of the *Loxoconcha* species. Type localities of new species circled.

species; strength of their shell possibly being effected by their shape, for example, the rather rotund genus *Xestoleberis.* Here, all the species described live on weed or in algae on lagoon terraces, within lagoon channels or on the more open nearshore shelf environment, and as such are subjected to the considerable tidal influences of the region. For details of the oceanography of the region the reader is referred to Evans *et al.* 1973 from which the following information has been taken:

Tides –maximum rise of 2·5 m in front of the islands to 1 m at the back of the lagoon—except during periods of prolonged onshore winds.
Water depth –up to 7 m deep in the lagoon channels and rarely exceeding 2 m on the lagoon terraces; often becoming dry at low tide.
Salinity –nearshore waters range from 42·7‰ to 44·5‰: lagoon waters range from 53·6‰ to 66·9‰. Higher values have been recorded from tidal pools but no species of *Loxoconcha* or of *Epakroconcha* have been obtained from these high salinity (77·4‰) pools.
Temperature –nearshore waters have a surface temperature of 23–24°C while lagoon waters range from 22–36°C.

Loxoconcha (Loxoconcha) multiornata sp. nov. (Fig. 11). This species of *Loxoconcha* is the most coarsely ornate of those present in our material. It is both a common nearshore shelf species and at the same time a common inhabitant of the more quiet higher salinity waters of the lagoon where it occurs both on the terraces and within the lagoon channels. This species thus shows no special preference for a particular environment. We did not, however, find any live specimens of *L. (L.) multiornata* and because of this there is a possibility that at least part of its distribution is due to postmortem dispersal. We consider that this would only be partially responsible for the distribution of the species as such a wide dispersal has not been observed for the other species.

Loxoconcha (Loxoconcha) gurneyi sp. nov. (Fig. 11). This species falls into the pattern of distribution expected of an ornate ostracod. The distribution of *L. (L.) gurneyi*, either as live specimens or dead valves, is restricted to the nearshore shelf environment. The presence of individuals just inside the mouth of the lagoon as well as on the tidal delta is to be expected through simple dispersal in a particularly high energy environment of both living and dead material. *L. (Loxoconcha) gurneyi* has also been recorded from beach sediments off the west coast of India by Jain (1978) see synonymy.

Loxoconcha (Loxoconcha) indica Jain (Fig. 11). A finely pitted species, *L. (L.) indica* is considered to be restricted solely to a lagoon environment. Live specimens have only been obtained from within Abu Dhabi lagoon where it lives on the outer and central lagoon terraces. It is not a common ostracod and the presence of a small number of dead valves on the nearshore shelf—significantly opposite the lagoon entrance—is considered to be due to postmortem dispersal. The original description of this species from beach sand from Mandvi, west coast India, is regarded as not being the true habitat for live specimens.

Loxoconcha (Loxoconcha) amygdalanux sp. nov. (Fig. 11). This species, like *L. (L.) indica,* is pitted but rather coarsely so. Indeed the intensity of the ornamentation is reflected by the dispersal of the species being equally dominant both on the nearshore shelf and within the channels and terraces of the outer and inner lagoon. The species has also been recorded by Paik (1977) from the Central Basin, Persian Gulf and from the Gulf of Oman. *L. (L.) amygdalanux* is thus considered to be tolerant of both high and low energy environments as well as tolerating a range of salinity and temperature gradients.

Loxoconcha (Epakroconcha) batei sub. gen. et sp. nov. (Fig. 11). The recorded distribution here represents our total knowledge of this species. Although live specimens were restricted to sample 1094, the type locality, the distribution of the species is not considered to be far removed from that shown here. The presence of dead valves outside the lagoon and possibly of those just inside the entrance is considered to be due to postmortem dispersal. The species is regarded as being restricted to the inner and central lagoon terraces, inhabiting a shallow water environment where a thin layer of filamentous algae often covers the sediment.

Conclusions

Apart from *Loxoconcha (L.) multiornata* the species of *Loxoconcha* exhibit the pattern of distribution that relates the degree of ornamentation to the energy level of the environment: the finest ornamented form (*L. (L.) indica*) being restricted to a lagoon environment and the more coarsely ornamented species (*L. (L.) gurneyi*) being restricted to the nearshore shelf, more open sea environment. *L. (L.) amygdalanux*, intermediate in the strength of its ornamentation, has a distribution equally shared between the outer part of the lagoon and the shelf environment outside. *L. (Epakroconcha) batei*, although rather coarsely ornamented, is the only species currently placed in this subgenus and in the absence of other species we cannot draw any conclusions from its restriction to a lagoon environment.

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A revision of the spider genus *Cocalus* (Araneae: Salticidae)

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Introduction

Cocalus Koch 1846 is a small genus of oriental and Australian Salticidae comprised of four known species, one of which is described here as new. Although the type species, *Cocalus concolor* Koch, is only known from a single adult male which has lost both palps, it is thought the low elevation on the carapace, shared by all species is sufficiently characteristic to unite the species here included in *Cocalus*. In the only known female (*C. murinus* Simon) the epigyne is dark with a median orifice and is not especially characteristic when compared with epigynes of related genera. However, the male palps (in the two species, *C. gibbosus* sp.n., and *C. limbatus* Thorell, for which these are known) are distinctive, the sinuous finger-like protuberance of the tibiae being, as far as I am aware, unique within the Salticidae.

Opisthoncus Koch from Australia is the only other genus known to the author to have a similar elevation on the carapace. It does not, however, appear to be closely related to *Cocalus* as the eye patterns are different, the elevation is situated between the posterior lateral eyes and the palps are less complex. The biology of *Cocalus* is unknown.

The standard abbreviations and measurements are those used by Wanless (1978*a*), but for the leg spination the system adopted is that used by Platnick and Shadab (1975).

Genus *COCALUS* Koch

Cocalus Koch, 1846 : 180, 230. Type species *Cocalus concolor* Koch, by subsequent designation (Simon, 1901 : 408). Koch, 1850 : 48. Marschall, 1873 : 393. Scudder, 1882 : 72. Peckham & Peckham, 1885 : 266, 288. Simon, 1901 : 405, 407, 408. Sherborn, 1922 : 1375; 1932 : 345. Petrunkevitch, 1928 : 181. Neave, 1939, I : 778. Roewer, 1954 : 934. Bonnet, 1956 : 1173.

Cocala: Simon, 1864 : 327, [lapsus calami]. Waterhouse, 1912 : 61. Neave, 1939 I : 778.

DEFINITION. Medium to large spiders ranging from about 7·5 to 8·6 mm in length. Sexual dimorphism not marked. *Carapace*: characteristic of genus, profile generally as in Figs 2A, B; 3A, B; moderately high, longer than broad, widest between coxae II–III, lateral margins usually with membraneous margin; fovea moderately long, situated just behind posterior lateral eyes; positioned centrally within posterior ocular quadrangle a small bump (arrowed in Fig. 2A, B, E). *Eyes*: set on moderately well developed tubercles, with black surrounds that are normally covered in hairs; arranged in three transverse rows comprised of anterior medians and anterior laterals, posterior medians, and posterior laterals; anteriors subcontiguous with apices strongly procurved in frontal view and recurved in dorsal view; anterior medians largest, anterior laterals about half diameter of anterior medians; posterior medians relatively large, positioned more or less midway between anterior laterals and posterior laterals and outside optical axis of anterior laterals; posterior laterals about as large as anterior laterals, set close to lateral margins of carapace when viewed from above; quadrangle formed by posterior median and posterior lateral eyes broader than long and widest posteriorly; entire quadrangle (measured from between bases of anterior medians to posterior margins of posterior lateral eyes) occupying between 45 and 47 per cent of carapace length. *Clypeus*: between 32 and 64 per cent of diameter of anterior median eyes, usually clothed in hairs. *Chelicerae*: robust, more or less parallel, slightly inclined anteriorly;

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promargin with three teeth, retromargin with four or five. *Maxillae and labium*: more or less as in Fig. 3D; bases usually obscured by coxae I. *Sternum*: elongate scutiform, generally as in Fig. 3E. *Coxae*: robust; coxae IV largest, others subequal. *Pedicel*: short. *Abdomen*: long and tapered; spinnerets long, posteriors robust and almost twice as long as robust anteriors, medians slender and slightly shorter than anteriors; anal tubercle a well developed cone; tracheal system not examined; spiricle an indistinct transverse slit near base of anterior spinnerets; former position of colulus apparently indicated by patch of hairs. *Legs*: moderately long and robust; spines strong and numerous; legs I sometimes with scanty ventral fringes on metatarsi and tibiae, also minute ventral setae on tarsi and metatarsi (c.f. *Portia* Karsch); claws pectinate, tufts present, scopulae absent. *Female palps*: moderately long and robust with terminal claw. *Male palps*: large, moderately complex and morphologically similar; densely clothed in hairs (not always shown in figures). Tibiae with truncate ventral apophysis and large retrolateral apophysis containing a sinuous finger-like protuberance of the tibiae (Fig. 4C); cymbium with basal retrolateral lobe; embolus (e) robust, arising from distal end of tegulum and curving inwards towards the alveolar cavity; near embolic base an indistinct sclerite (a), also arising from embolic base a translucent lobe (l); tegulum (t) ovoid with tegular furrow (f), retrolateral striae and dark peripheral seminal ducts (Fig. 40). *Epigyne*: large and dark, median orifice plugged in specimen examined. Internal structure not examined.

REMARKS. Platnick (pers. comm.) suggested that the tegular furrow of *Phaeacius* (see Wanless, 1981) and related genera may contain pores, as the furrow and striae resembled distribution channels which may spread a secretion over the surface of the tegulum (Fig. 1A, B). A re-examination of the male palp of *Phaeacius fimbriatus* Simon, confirmed Platnick's suggestion by showing the presence of a single minute pore in the wall of the furrow (position arrowed in Fig. 1A). The pore, which seems disproportionately small in relation to the size of the furrow, cannot be resolved with the stereoscopic microscope. Unfortunately there is insufficient material to confirm the presence of pores in *Cocalus*.

AFFINITIES AND DIAGNOSIS. *Cocalus* belongs to a group of genera in which the male palps are characterized by the presence of a tegular furrow and truncate or obtuse apophysis of the venter of the tibiae. It is readily distinguished from other genera of this group (i.e. *Boethus* Thorell, *Brettus* Thorell, *Codeta* Simon, *Cyrba* Simon, *Phaeacius* Simon and *Portia* Karsch) by the presence of an elevation in the posterior ocular quadrangle (Fig. 2A, B, E).

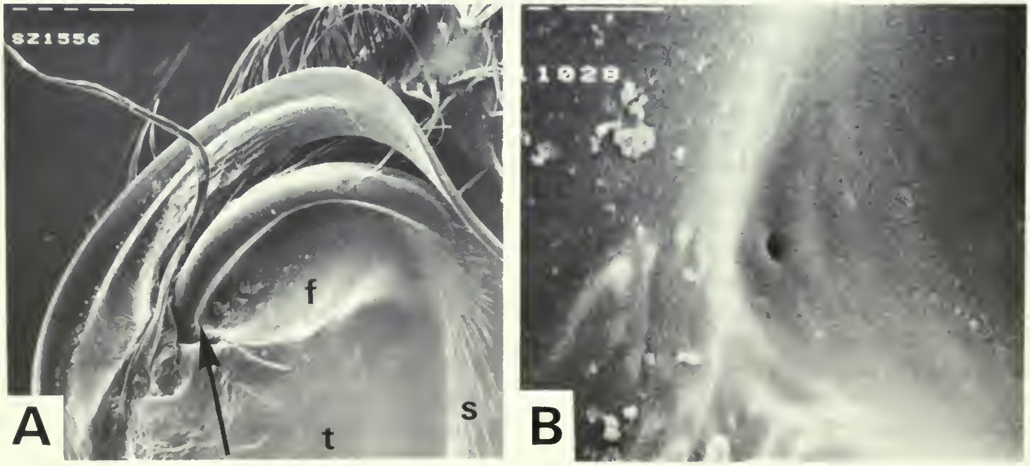

Fig. 1 *Phaeacius lancearius* (Thorell), ♂ palp: A, apical region, × 60, showing tegulum (t), tegular furrow (f) and striae (s); location of pore indicated by arrow. B, pore in wall of tegular furrow, × 1200.

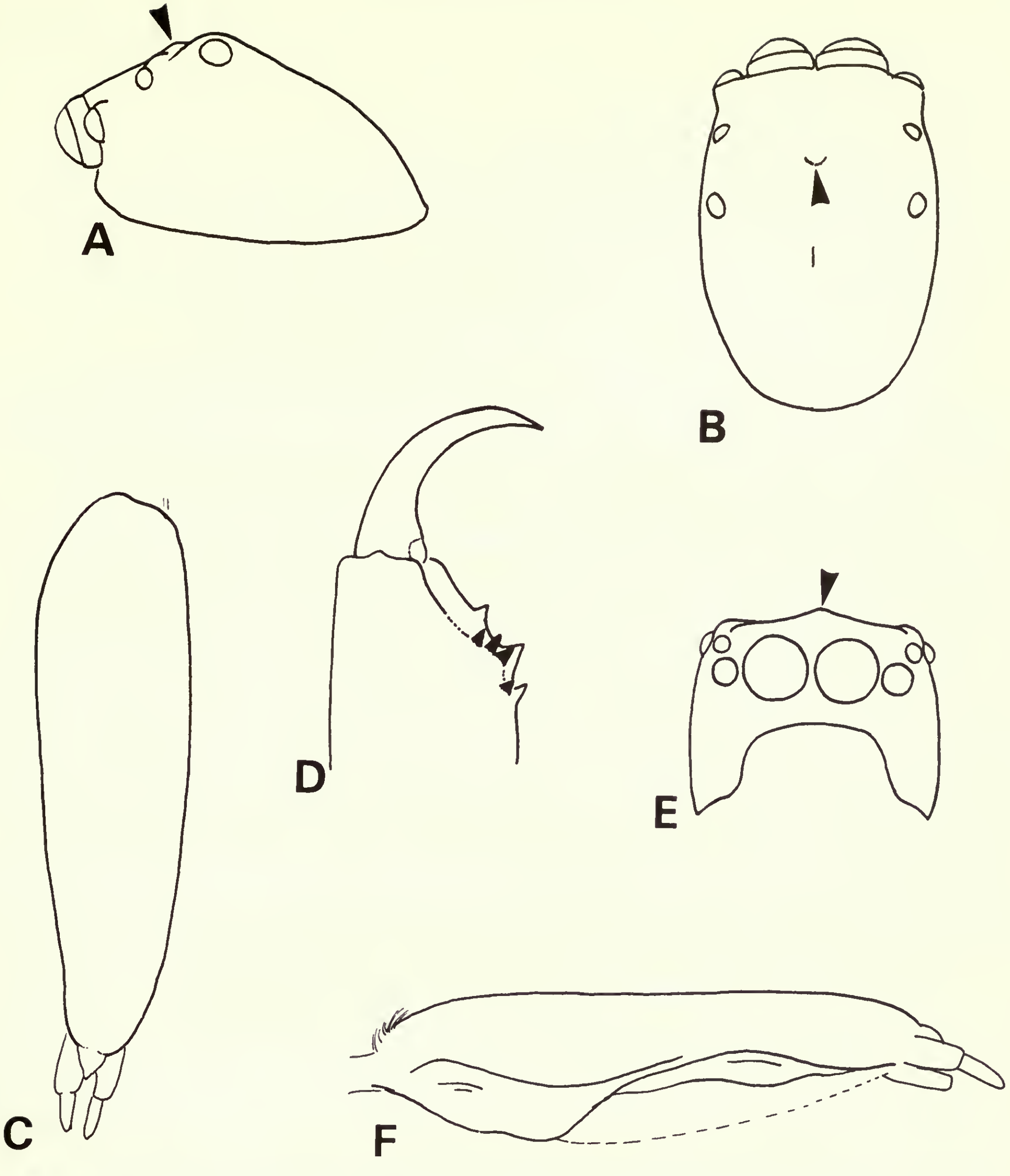

Fig. 2 *Cocalus concolor* Koch, holotype ♂: A, carapace, lateral; B, carapace, dorsal; C, abdomen, dorsal; D, chelicera, inner view; E, carapace, facies; F, abdomen, lateral.

List of species in the genus *Cocalus* Koch, 1846

Cocalus concolor Koch, 1846
C. gibbosus sp. n.
C. limbatus Thorell, 1878
C. murinus Simon, 1899

Summary of taxonomic changes effecting species listed in the catalogues of Roewer (1954) and Bonnet (1956) as belonging in *Cocalus*.

Cocalus africanus Thorell, junior synonym of *Portia africana* (Simon) (Wanless 1978*b*)

Cocalus lancearius Thorell, transferred into *Phaeacius* Simon (Roewer 1954), redescribed (Wanless 1981).

Cocalus longipes Thorell, *Cocalus macellus* Thorell and *Cocalus protervus* Thorell all belong in *Cocalodes* Pocock, **comb. n.**

Cocalus salax Thorell, belongs in *Codeta* Simon, **comb. n.**

The synonyms listed by Bonnet (1956) are accepted, but for one species, *Phaeacius ramipalpis* (Thorell) which evidently belongs in *Boethus* (see Wanless 1981). *Cocalodes, Codeta* and *Boethus* are presently being revised by the author.

***Cocalus concolor* Koch**

(Fig. 2A–F)

Cocalus concolor Koch, 1846 : 180, ♂. Holotype ♂, Indonesia, Bintang Island (MNHU, Berlin) [examined]. Koch, 1850 : 49. Thorell, 1892 : 475. Simon, 1896 : 351; 1901 : 407, 408. Rainbow, 1898 : 352. Petrunkevitch, 1928 : 181. Roewer, 1954 : 935, Bonnet, 1956 : 1173. Prószyński, 1971 : 390. Wanless, 1978*b* : 85.

Cocala concolor: Simon, 1864 : 327. [lapsus calami].

DIAGNOSIS. The holotype of this species, a male in poor condition, has no palps and a diagnosis cannot be given at the present time.

FEMALE. Unknown, but *C. murinus* Simon from Sumatra may belong here.

MALE HOLOTYPE. In poor condition with carapace and legs translucent. *Carapace* (Fig. 2A, B): brown, irregularly clothed in recumbent white hairs; punctate with iridescent violet sheen in eye region. *Eyes* (Fig. 2A, B, E). *Clypeus*: with light brownish hairs below AM, densely white haired below AL. *Chelicerae*: dark brown with long light brown and black hairs; teeth as in Fig. 2D. *Maxillae, labium and sternum*: more or less as in *C. murinus* (Fig. 3D, E); brownish. *Abdomen* (Fig. 2C, F): dark brown. *Legs*: detached, some missing; brownish. *Palps*: missing.

Dimensions (mm): total length *c.* 7·5; carapace length 3·0, breadth 2·12, height 1·82; abdomen length 4·48; eyes, anterior row 1·9, middle row 1·90, posterior row 1·96; quadrangle length 1·42. *Ratios*: AM : AL : PM : PL :: 14 : 7·5 : 5 : 7; AL–PM–PL :: 12–11·5; AM : CL :: 14 : 8.

DISTRIBUTION. Indonesia, Bintang Island.

MATERIAL EXAMINED. Holotype ♂, data given in synonymy.

REMARKS. Rainbow (1898) records this species from British New Guinea, but gives no details as to the precise locality, neither does he indicate the sex of the specimen concerned. For the present it seems best to regard this record with caution and not formally include it in the distribution list.

***Cocalus murinus* Simon**

(Fig. 3A–E)

Cocalus murinus Simon, 1899 : 102, ♀. LECTOTYPE ♀ (here designated) Indonesia, Sumatra (MNHN, Paris) [examined]. Simon, 1901 : 406, 407. Roewer, 1954 : 934. Bonnet, 1956 : 1173. Prószyński, 1971 : 391.

DIAGNOSIS. Other females of *Cocalus* are unknown and a diagnosis cannot be given at the present time. Previous studies on *Portia* and *Phaeacius* suggest that the epigynes of *Cocalus* may be difficult to distinguish from one another.

MALE. Unknown, but possibly synonymous with the type species *C. concolor* from Bintang Island.

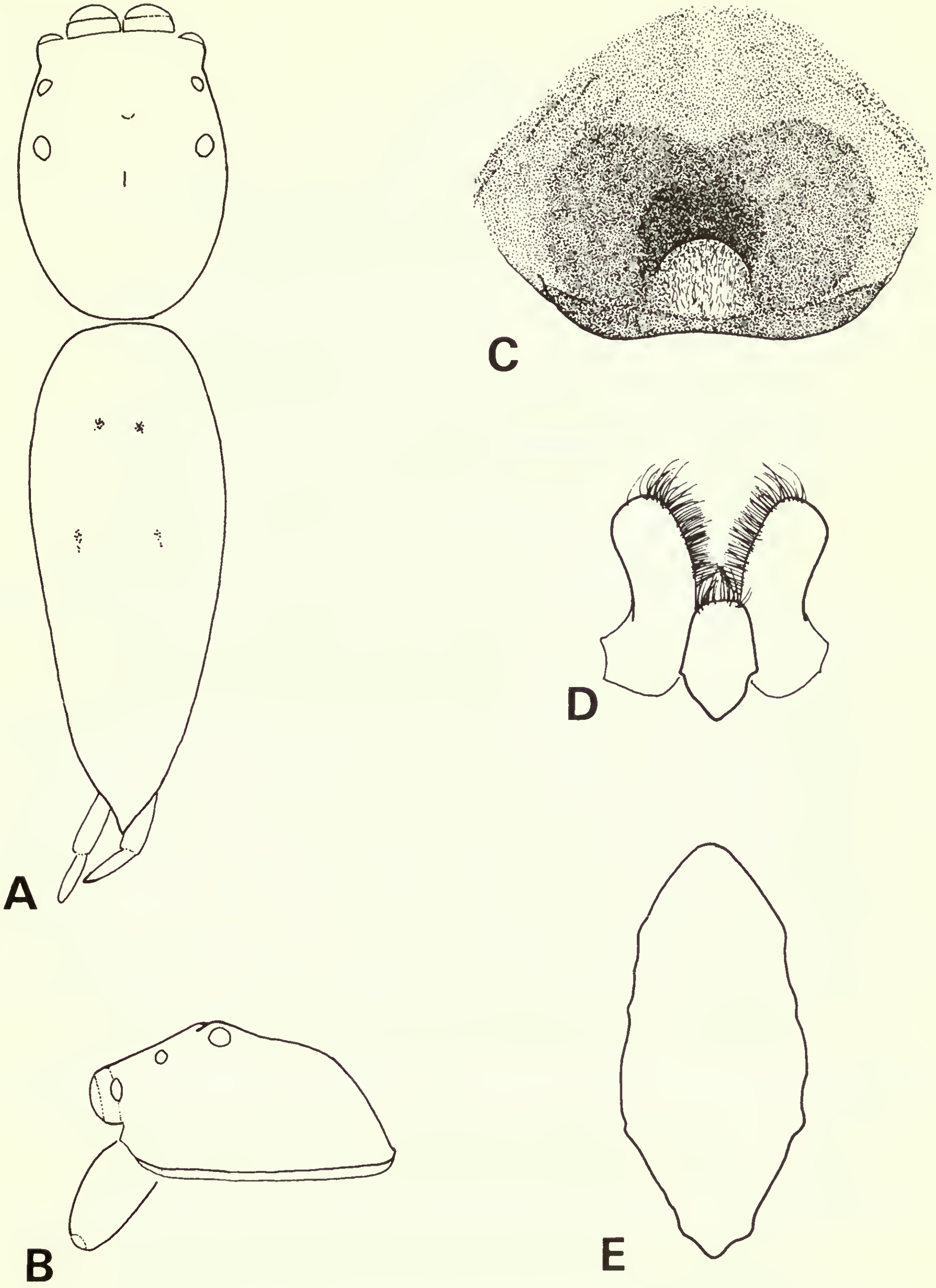

Fig. 3 *Cocalus murinus* Simon, lectotype ♀: A, dorsal view; B, carapace, lateral; C, epigyne; D, maxillae and labium; E, sternum.

FEMALE LECTOTYPE. In fair condition. *Carapace* (Fig. 3A, B): amber with vague markings radiating from foveal region; irregularly clothed in short recumbent white hairs (rubbed). *Eyes*: with black surrounds, fringed in white hairs. *Clypeus*: clothed in long white hairs. *Chelicerae*: amber, shiny with long white hairs basally; promargin with three teeth, retromargin with five. *Maxillae and labium* (Fig. 3D): orange-brown with inner maxillae margins and labial tip yellowish. *Sternum* (Fig. 3E): yellow-brown tinged black, shiny; clothed in long coarse white hairs and fine pale brown ones. *Abdomen*: rubbed; dull whitish yellow with sooty lateral markings, pattern indistinct; spinnerets yellow-brown. *Legs*: pale amber to light yellowish orange; spination of legs I: metatarsi v 2–0–0, p 0–1–0, d 2–1–1, r 0–1–0; tibiae v 2–2–2, p 1–0–1, d 1–1–1, r 1–0–1; patellae p 1–0–0, r 1–0–0; femora d 0–2–4. *Palp*: light yellowish orange to pale amber. *Epigyne* (Fig. 3C): dark amber clothed in creamy hairs, orifice indistinct and evidently plugged.

Dimensions (mm): total length 8·56; carapace, length 3·36, breadth 2·52, height 1·88; abdomen length 5·6; eyes, anterior row 1·96, middle row 2·02, posterior row 2·16; quadrangle length 1·54. *Ratios*: AM : AL : PM : PL :: 15·5 : 8 : 5 : 8; AL–PM–PL :: 12–12·5; AM : CL :: 15·5 : c. 5 (too hairy for accurate measurement).

DISTRIBUTION. Indonesia, Sumatra.

MATERIAL EXAMINED. Lectotype ♀, **Sumatra** (*J.-L. Weyers*) (MNHN, Paris, 16290).

Cocalus gibbosus sp. n.

(Fig. 4A–D)

DIAGNOSIS. Similar to *C. limbatus*, but distinguished by the truncate dorsal prong of the retrolateral tibial apophysis (Fig. 4C).

FEMALE. Unknown.

MALE HOLOTYPE. In good condition. *Carapace* (Fig. 4A, B): dark orange-brown; clothed in short recumbent white hairs. *Eyes*: with black surrounds except AM; fringed in whitish hairs. *Clypeus*: covered in dark grey hairs below AM with whitish hairs below AL. *Chelicerae*: dark orange-brown, sparsely covered in fine black hairs; promargin with three teeth, retromargin with four. *Maxillae*: brownish with dull white inner margins. *Labium*: dark brown tipped dull white. *Sternum*: brownish with black hairs. *Abdomen*: dorsally orange-brown to greyish brown, clothed in short recumbent white hairs (rubbed); pattern indistinct; venter dark greyish with vague longitudinal rows of lighter spots, clothed in short black hairs. *Legs*: generally orange-brown with whitish, and black hairs; spination of legs I: metatarsi v 2–0–0, p 1–1–0, d 0–1–1, r 1–1–0; tibiae v 2–2–2, p 1–1–0, d 1–1–1, r 2–1–0; patellae p 1–0–0, r 1–0–0; femora p 0–0–1, d 0–2–3. *Palp* (Fig. 4C, D): similar to that of *C. limbatus*, clothed in white hairs.

Dimensions (mm): total length 8·16; carapace, length 3·0, breadth 2·28, height 1·88; abdomen length 5·04; eyes, anterior row 1·78, middle row 1·88, posterior row 2·0; quadrangle length 1·38. *Ratios*: AM : AL : PM : PL :: 14 : 7 : 4·5 : 7; AL–PM–PL :: 14 : 9.

DISTRIBUTION. Australia.

MATERIAL EXAMINED. Holotype ♂, **Australia**, Lockerbie, N. Queensland (*R. Raven*) 30.i–1.ii.1975 Queensland Museum, reg. no. QM S846.

Cocalus limbatus Thorell

(Fig. 5A–D)

Cocalus limbatus Thorell, 1878 : 283, 311, ♂. Holotype ♂, Amboina (MCSN, Genova) [examined]. Thorell, 1881 : 492, 706. Simon, 1901 : 407. Roewer, 1954 : 934. Bonnet, 1956 : 1173. Prószyński, 1971 : 391.

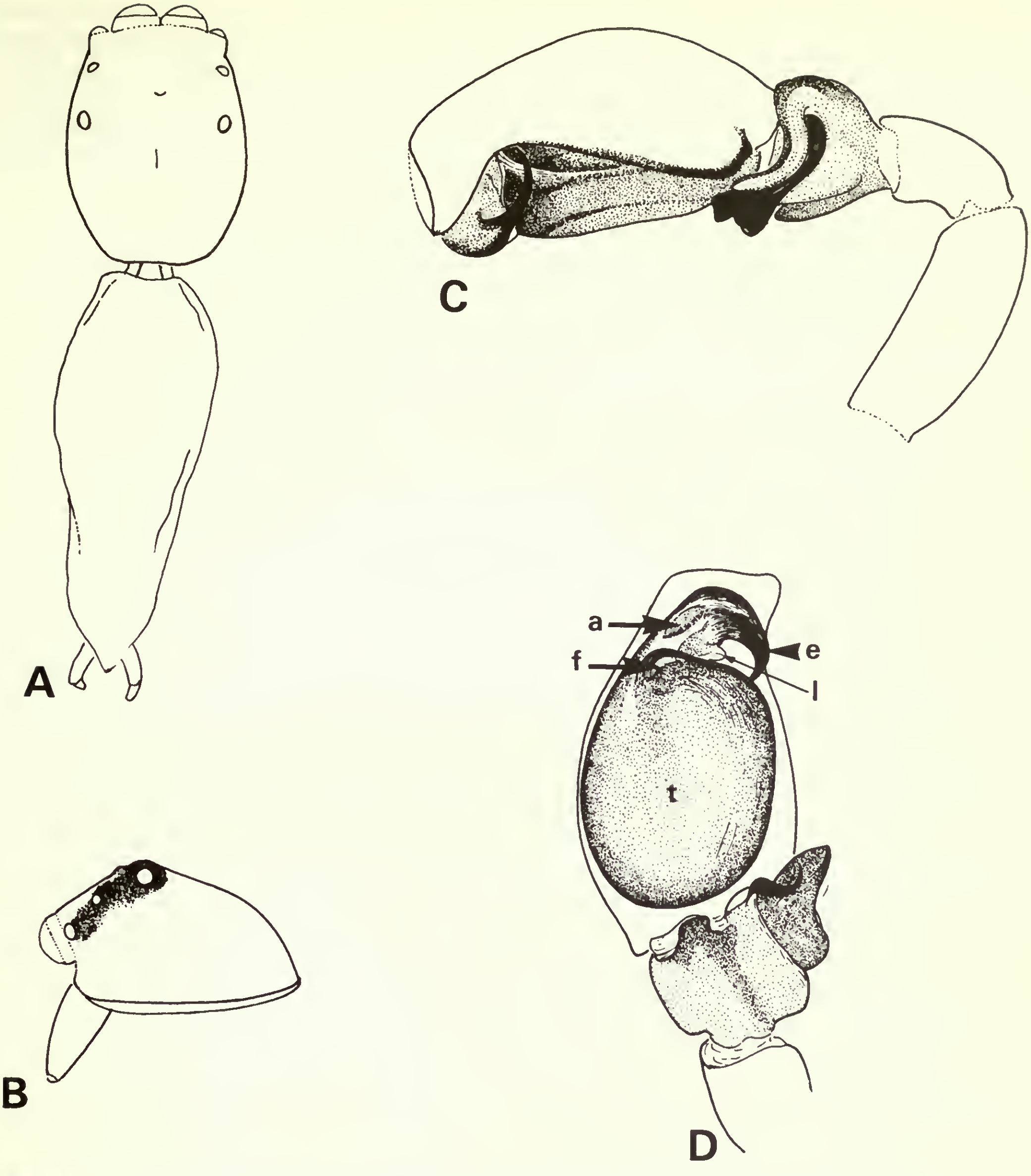

Fig. 4 *Cocalus gibbosus* sp. n., holotype ♂: A, dorsal view; B, carapace, lateral; C, palp, retrolateral; D, palp, ventral. Abbreviations: a, sclerite; e, embolus; l, lobe; f tegular furrow; t tegulum.

Diagnosis. Similar to *C. gibbosus*, but distinguished by the obtuse dorsal prong of the retrolateral tibial apophysis (Fig. 5C).

Female. Unknown.

Male holotype. In fair condition. *Carapace* (Fig. 5A, B): amber to dark amber, irregularly clothed in whitish pubescent hairs (rubbed). *Eyes*: with black surrounds except AM; fringed in whitish hairs. *Clypeus*: fringed in light brownish hairs below AM with white hairs below AL. *Chelicerae*: dark amber; thinly covered in pale amber hairs; teeth not examined. *Maxillae*: brownish amber with inner distal margins yellowish. *Labium*: dark amber.

Sternum: partly obscured by coxae, apparently similar in form to that of *C. murinus*; dark amber with pale amber hairs. *Abdomen*: dull brownish amber lightly tinged black (original markings bleached); a tuft of pale amber hairs anteriorly, otherwise irregularly covered in dull whitish hairs. *Legs*: generally amber; spination of legs I: metatarsi v 1–0–0, p 1–0–0, d 2–1–1, r 0–1–0; tibiae v 2–2–2, d 2–2–1, r 1–0–0; patellae p 1–0–0, r 1–0–0; femora d 0–2–4. *Palp* (Fig. 5C, D): the protuberance resting within the 'bowl' of the retrolateral tibial apophysis is slightly shorter than that found in *C. gibbosus*.

Dimensions (mm): total length 7·44; carapace, length 2·94, breadth 2·28, height 1·8; abdomen length 4·52; eyes, anterior row 1·92, middle row 1·96, posterior row 2·06; quadrangle length 1·4. *Ratios*: AM : AL : PM : PL :: 16 : 8 : 5 : 7; AL–PM–PL :: 11–11; AM : CL :: 16 : 6.

DISTRIBUTION. Indonesia, Amboina.

MATERIAL EXAMINED. Holotype ♂, data given in synonymy.

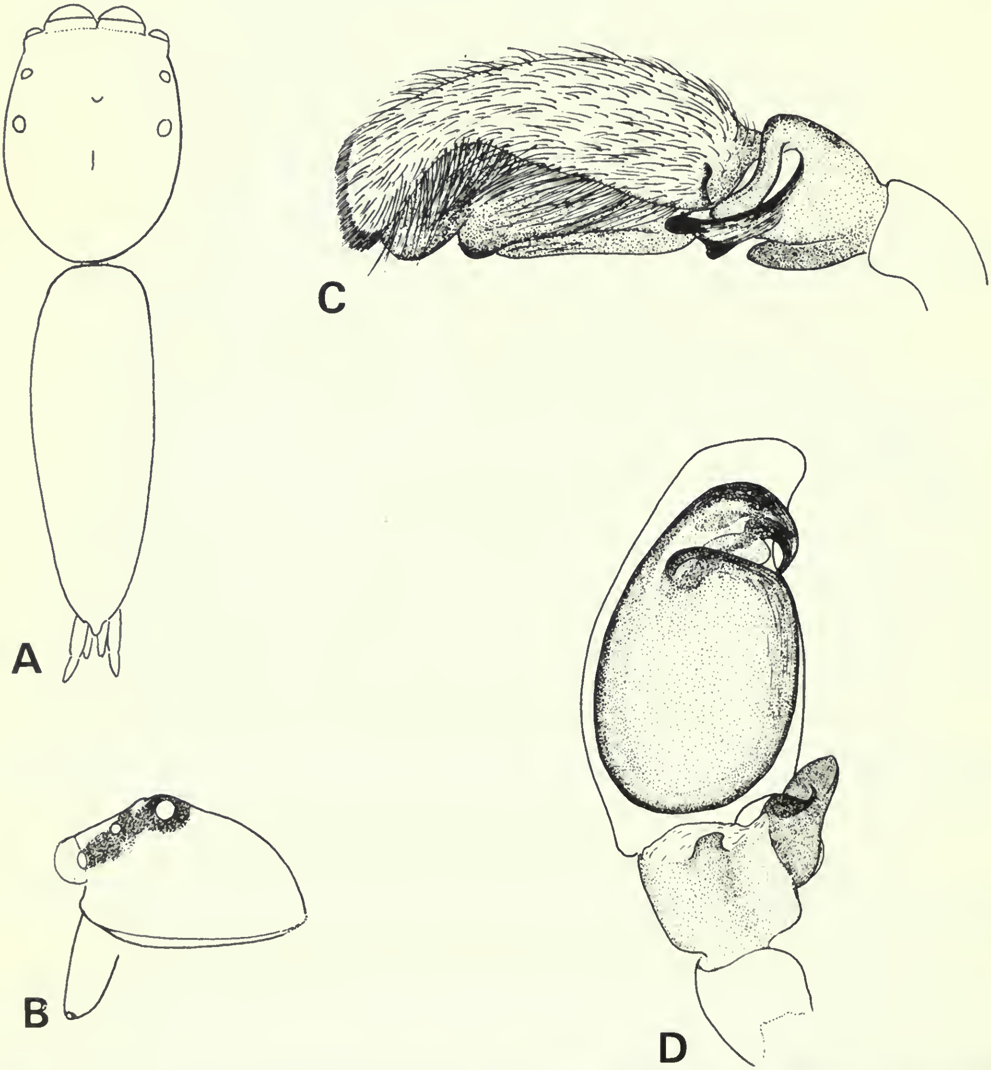

Fig. 5 *Cocalus limbatus* Thorell, holotype ♂: A, dorsal view; B, carapace, lateral; C, palp, retrolateral; D, palp, ventral.

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I wish to thank the following colleagues for providing specimens for study. Dr G. Arbocco, Museo Civico di Storia Naturale, Genova (MCSN, Genova); M. M. Hubert, Muséum national d'Histoire naturelle, Paris (MNHN, Paris); Dr M. Moritz, Zoologisches Museum, Berlin (ZM, Berlin); Dr Valerie Todd Davies, Queensland Museum, Brisbane (QM, Brisbane). Also Mr D. Macfarlane (CIE, London) for reading the manuscript.

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The *Phthiracarus* species of C. L. Koch

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Introduction

Koch (1841) described a number of species of *Hoplophora* from Regensburg, Germany, of which nine are currently classified in *Phthiracarus*: *crinita, ferruginea, globosa, laevigata, lentula, longula, lucida, straminea* and *testudinea* (Parry, 1979). Apart from the last mentioned species, which appears from Koch's original figure to have a greater affinity with the Euphthiracaroidea (but see Jacot, 1936), all are undoubtedly members of the genus *Phthiracarus*. These species are, however, extremely difficult to reidentify since Koch's very brief descriptions are based almost entirely on body shape and colour, two characters now known to be uniform in many species of this genus. Only *globosa* and *laevigata* can be characterized by body shape alone: in comparison with the other *Phthiracarus* species collected at Regensburg, *H. globosa* was said to be very 'globular' while the illustration of *H. laevigata* shows the notogaster to be 'angled' anteriorly.

Several redescriptions of Koch's species have been published, including those of Jacot (1936), Feider and Suciu (1957) and van der Hammen (1963). Jacot collected at more than 20 localities in the Regensburg area, recognizing six of Koch's species (*laevigata, testudinea, crinita, lentula, straminea* and *ferruginea*) and one new *Phthiracarus* species, *P. boresetosus*. Localities were chosen based not only on Koch's habitat descriptions but on Fürnrohr's detailed lists of the Regensburg flora published in 1839. Jacot treated the redescriptions in considerable detail, identifying each species on the basis of body shape and size, and setal form and length. However, he neglected to include details of the leg chaetotaxy which are now regarded as being essential for the separation of *Phthiracarus* species. Although Jacot's interpretations of *crinitus* and *lentulus* correspond with those of the present study, his specimens have not been considered for neotype designation, since all are entire, uncleared and mounted together with one or more other species in Canada Balsam. In this condition, Jacot's material would not easily withstand dismounting, dissection and remounting. Further collecting at Regensburg by van der Hammen in 1959 and 1961 resulted in his description of *P. laevigatus* and the designation of a neotype. A number of other species were tentatively identified by van der Hammen (pers. comm.) as representing Koch's seven other species—this material has been examined as part of the present study. Material collected by the late Dr Max Sellnick at Regensburg, and made available to the author through the courtesy of Dr Gisela Rack, Hamburg, has also been examined in an attempt to determine the identities of Koch's *Phthiracarus* species. Unfortunately, it has not been possible to borrow any of the specimens studied by Feider and Suciu.

Family **PHTHIRACARIDAE** Perty, 1841

Phthiracarus crinitus (C. L. Koch)
(Figs 1–7)

Hoplophora crinita Koch, 1841* : Heft. 32, t. 8. Regensburg [type series presumed lost]. NEOTYPE (here designated), Schweighauser Forest, Regensburg (ZM, Hamburg, A30/80).

Phthiracarus crinitus: Jacot, 1936 : 172 [in part]. Topotypes, Dechbetten Forest, Regensburg (MHN, Geneva, 3119h) [examined]; Willmann, 1931 : 130.

*The dating for the various Hefte follows Sherborn (1923).

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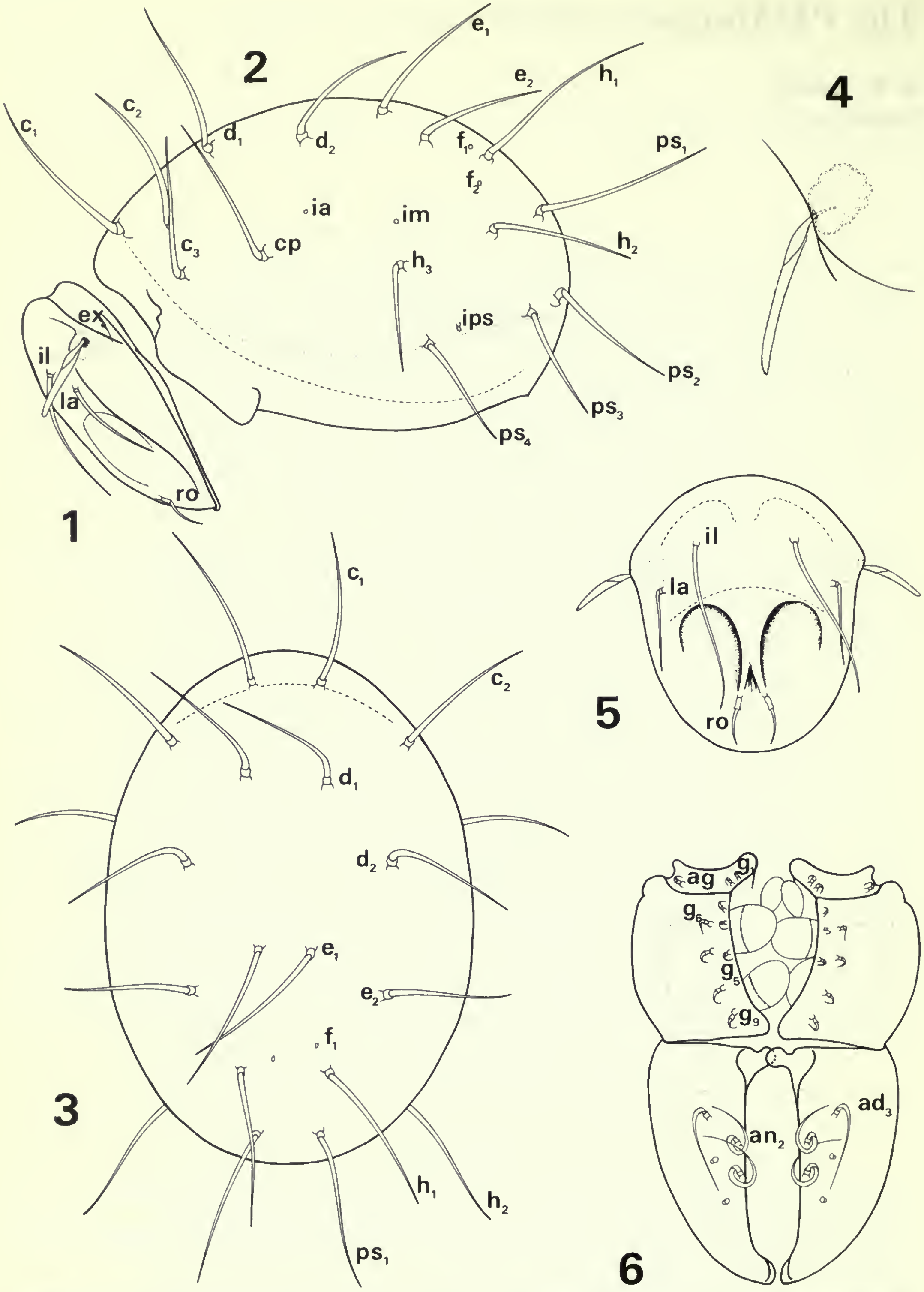
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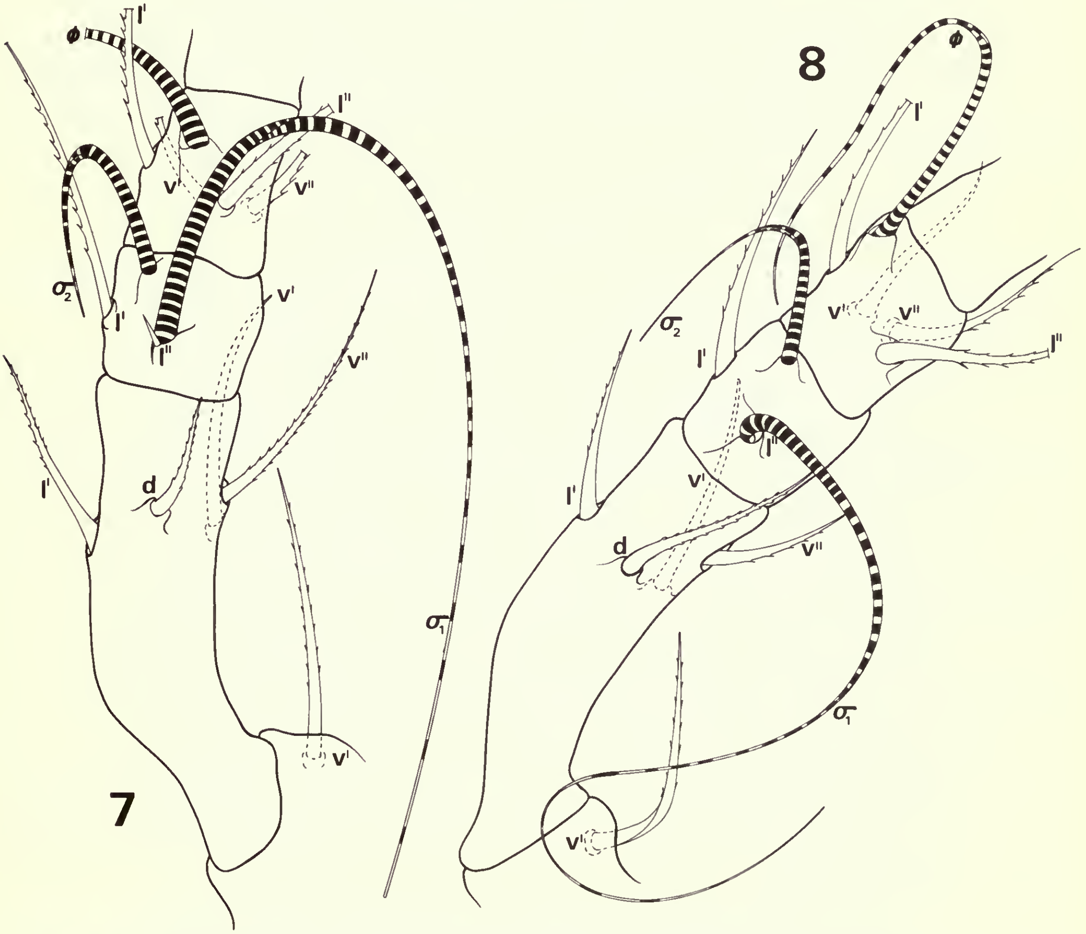
Figs 1–6 *Phthiracarus crinitus*: (1) aspis, lateral; (2) notogaster, lateral; (3) notogaster, dorsal; (4) sensillus; (5) aspis, dorsal; (6) ano-genital region.

ADULT: Large and strongly sclerotized. The *aspis* (Figs 1, 4–5) ranges in length from 255–330 μm with a maximum width of 220–270 μm. All the dorsal setae are long, simple and procumbent. The interlamellar setae (*il*) which are inserted just posterior to the bothridia, are about 1·5 times the length of the lamellars (*la*) and extend to the rostral bases. Setae (*ro*) almost reach the anterior aspal margin. The sensilli are 60–100 μm in length and expanded basally—the distal portion is slender, serrated and blunt terminally. The exobothridial setae (*ex*) are short. The *notogaster* (Figs 2–3), 480–550 μm long (measured along a line through c_1–ps_1) and with a greatest depth of 330–390 μm, is elongate in lateral aspect. All the notogastral setae are long (greater than the distance c_1–d_1) and simple, the *c* and *d* series being erect while those in the *e, h* and *ps* series are recurved. Seta c_1 is situated on the posterior margin of the collar and setae c_{2-3} submarginally. Vestigial f_1 is located just dorsal to the seta h_1 while the fissures *ip* and *ips* are situated between setae h_2 and h_3 and between setae ps_3 and ps_4 respectively. On each *anal plate* (Fig. 6) there are three setae of more or less equal length (an_{1-2} and ad_3). The nine genital setae are arranged in two rows, an anterior marginal row of five setae (g_{1-5}) and a posterior submarginal row of four (g_{6-9}). A single aggenital seta *ag* is located antiaxially in the genital furrow. The genital papillae are typically phthiracaroid in form, the anterior pair being considerably smaller than the two posterior pairs. The *chelicerae* are 180–210 μm long with about 20 sharply pointed spines on the paraxial surface



Figs 7–8 Leg I, trochanter to tibia, dorsal aspect: (7) *Phthiracarus crinitus*; (8) *Phthiracarus globosus*.

of the principal segment and about 25 conical spines antiaxially. The *leg chaetotaxy* is of the 'complete type' (see Parry, 1979) with four setae on femur I and a single seta on genu IV. All the solenidia are long and more or less straight. On tarsus I the seta coupled with solenidion ω_2 is short and barely discernible. Setae (*tc*) and (*u*) on this segment, and (*tc*), (*u*), (*p*) and *s* on tarsi II–IV are ribbon-like, hooked distally and covered with whorls of spicules in the middle third. The four setae on femur I (Fig. 7), *d*, (*v*) and *l′*, are all located at about the same level on the segment. Seta *d* which is the shortest of the four (about two-thirds as long as *l′*), is thickened, bluntly serrated and somewhat curved.

MATERIAL: Three specimens from a sample (no. 59015) of moss and bilberries (*Vaccinium myrtillus*), Schweighauser Forest, Unterkaulhausen, Regensburg, 19.vii.1959 (M. Sellnick), deposited in the collections of the Zoological Museum of the University of Hamburg. One of these specimens (A30/80) is hereby designated as the ***neotype***. Other material was examined from rotten wood and litter beside a brooklet (sample no. 61 R45), Donaustaufer Forest, Regensburg, 27.vi.1961 (L. van der Hammen) (RNH, Leiden). *P. crinitus* was not widespread in the Regensburg material, being present only in small numbers in the above two samples.

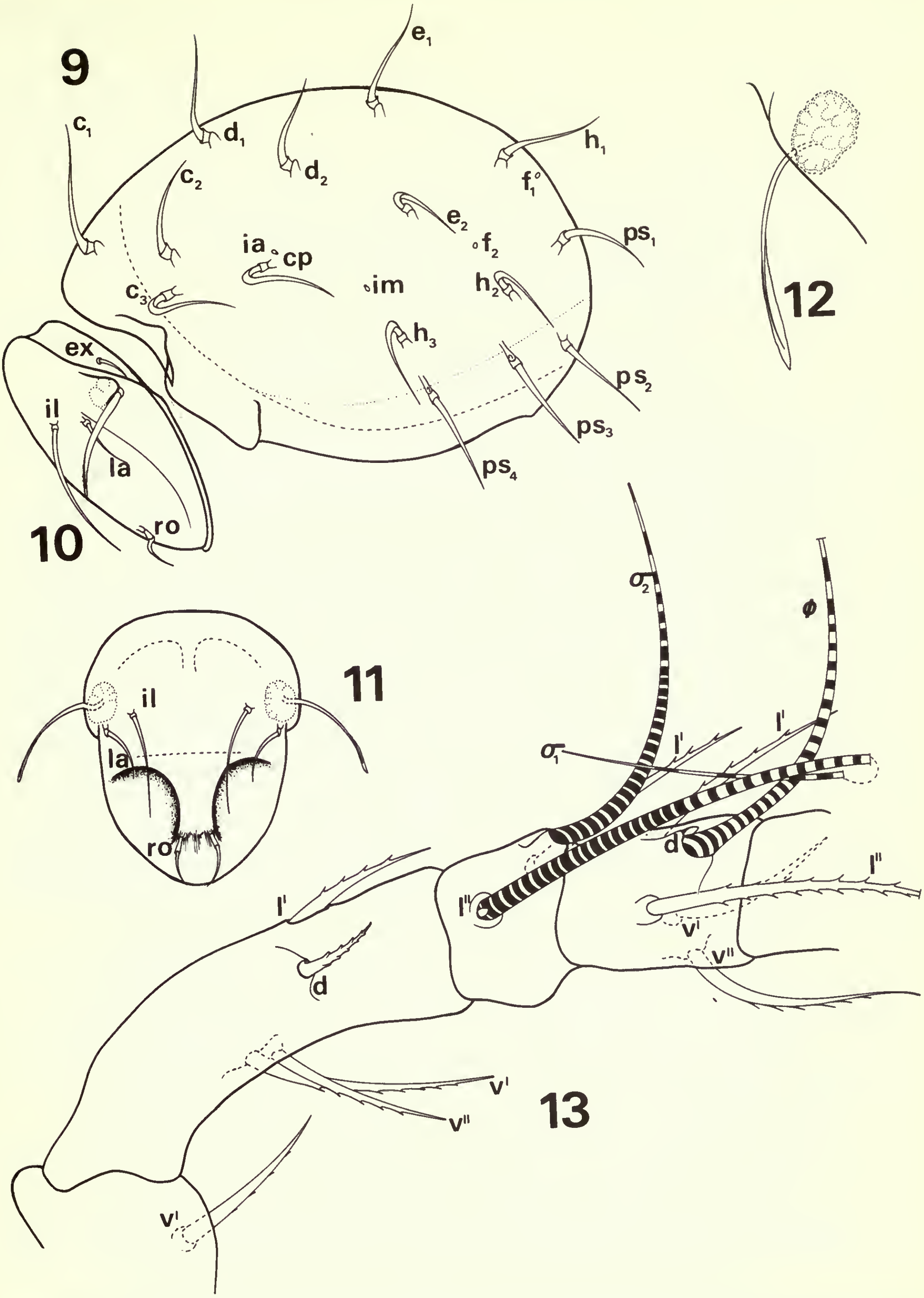
REMARKS: Koch recorded *crinita* predominantly in mosses, Regensburg. Although the original description of the species was rather incomplete, *crinita* appeared to be characterized by unusually long notogastral setae—a feature which was noted by Jacot (1936) in his description of specimens which he considered to be conspecific with *H. crinita*. Jacot's specimens are for the most part conspecific and in good condition. However, as mentioned above, they have not been considered for neotype designation. A neotype was selected from amongst Sellnick's spirit specimens which were found to be conspecific with the mite described by Jacot.

Phthiracarus ferrugineus (C. L. Koch)
(Figs 9–13)

Hoplophora ferruginea Koch, 1841: Heft. 32, t. 10. Regensburg [type series presumed lost]. NEOTYPE (here designated), Taimering, Regensburg (RNH, Leiden, P2005–7).
[*Phthiracarus ferrugineus*: Jacot, 1936 : 179. Misidentification, see under *P. longulus*.]

ADULT: Rather small and weakly sclerotized. The *aspis* (Figs 10–12) is about 225 μm in length with a greatest width of about 160 μm. The rostrals (*ro*) are short and do not reach the anterior aspal margin. Setae (*il*) are twice the length of setae (*la*) and extend to the rostral bases. The sensilli are long (70–80 μm), slender and distally serrated. The exobothridial setae (*ex*) are short. The *notogaster* (Fig. 9), about 350 μm in length, has a maximum depth of about 270 μm and bears moderately long (more or less equal to the distance c_1–d_1), simple setae which are erect to recurved. Setae c_1 and c_3 are inserted close to the posterior collar margin and seta c_2 submarginally. Vestigial f_1 is located one-third of the distance between setae h_1 and ps_1. Only the fissures *ia* and *im* appear to be present. On each *anal plate* there are three setae (setae ad_{1-2} vestigial) of which an_{1-2} are the longest. The *chelicerae* are 135–140 μm long with 9 to 10 sharply pointed spines on the paraxial surface of the principal segment and 6 to 10 conical spines antiaxially. The *leg chaetotaxy* is of the 'complete type' with rather short and straight solenidia. On femur I (Fig. 13) seta *d* is short (about half as long as *l′*), thickened and, as in *crinitus*, this seta is curved and bluntly serrated. In the three available specimens, the setal arrangement on this segment shows considerable variation. In the neotype (Fig. 13) seta *d* is located on a level with seta *l′* and anterior to the ventral setae, while in a second specimen *d* is located anterior to the lateral seta, and in a third specimen, posterior to the lateral seta.

MATERIAL: Three specimens from rotten material in a moist hayfield, Taimering, Regensburg, 19.vi.1961 (L. van der Hammen) (sample no. 61 R34), deposited in the collections of the Rijksmuseum van Natuurlijke Historie, Leiden. One of these specimens (P2005–7) is hereby designated as the ***neotype***.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Figs 9–13 *Phthiracarus ferrugineus*: (9) notogaster, lateral; (10) aspis, lateral; (11) aspis, dorsal; (12) sensillus; (13) leg I, trochanter to tibia, dorsal aspect.

REMARKS: Koch recorded *ferruginea* in mosses on trees. He described the species as being very small with long, fine notogastral setae and from his figure it is evident that the species possessed rather long and prominent sensilli.

The smallest of the Regensburg species examined in the present study, *P. ferrugineus* (notogastral length 350 μm) is somewhat unusual in its possession of four setae on femur I and a single seta on genu IV, two features which are associated with larger species (notogastral length 500–1000 μm) of the genus. Smaller species with a notogastral length of less than 500 μm are generally characterized by a 'reduced' form of leg chaetotaxy.

Although rather smaller, *P. ferrugineus* bears considerable resemblance to *P. membranifer* Parry (notogastral length 310–500 μm) recorded from the fermentation layer under Sitka spruce, Tintern Forest, Monmouthshire. In comparison with the latter, *P. ferrugineus* differs only in having a 'complete' form of leg chaetotaxy.

Phthiracarus globosus (C. L. Koch)
(Figs 8, 14–18)

Hoplophora globosa Koch, 1841 : Heft. 32, t. 12. Regensburg [type series presumed lost]. NEOTYPE (here designated), Burgweinting, Regensburg (ZM, Hamburg, A31/80).

Phthiracarus globosus: Willmann, 1931 : 193; Feider & Suciu, 1957 : 5; Sellnick, 1960 : 131.

Phthiracarus globus Parry, 1979 : 341. Holotype, Rydal Water, Westmorland, England (BMNH, London, 1976.2.18.3.) [examined]. **Syn. nov.**

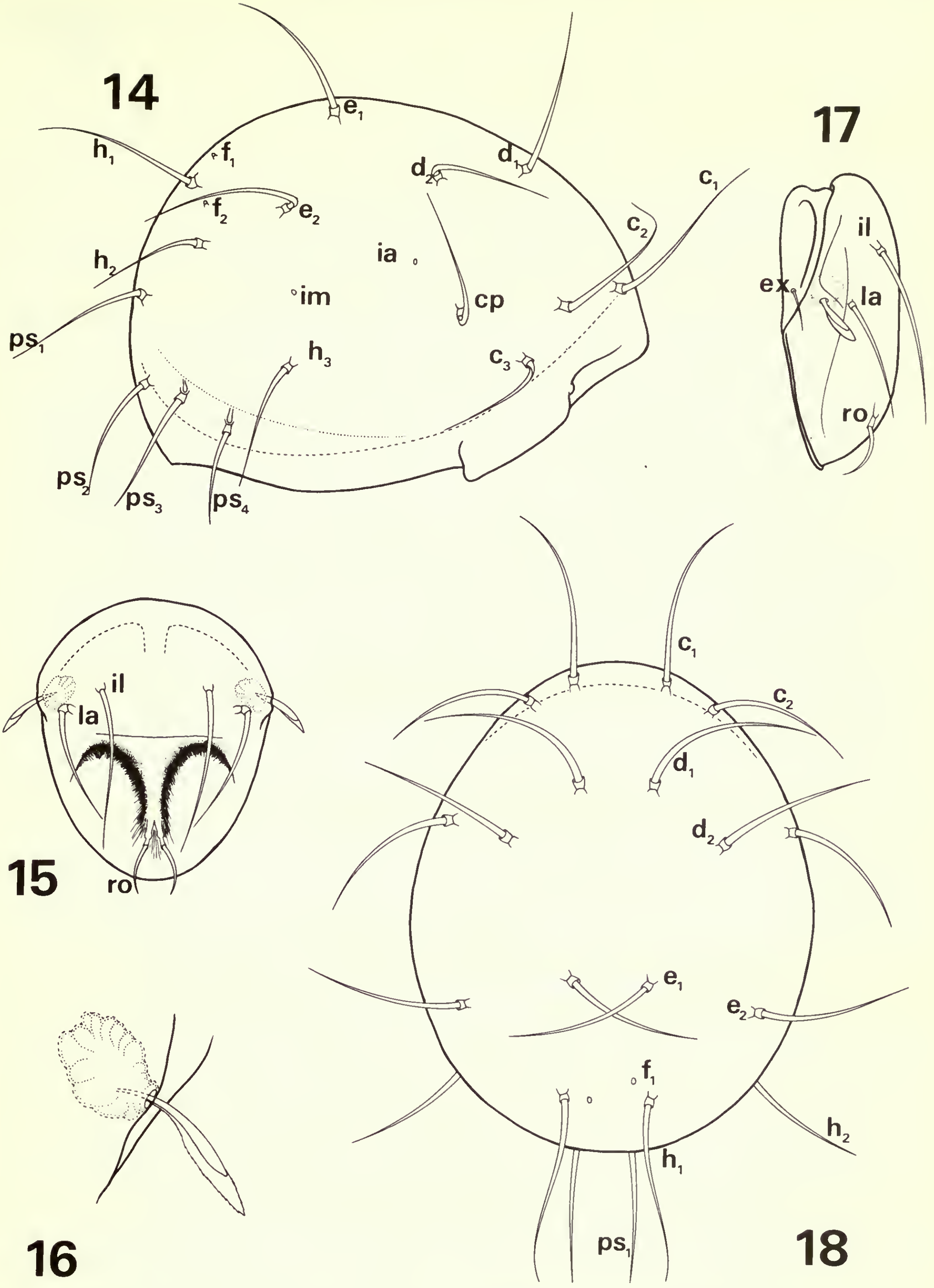
ADULT: Large and strongly sclerotized. The *aspis* (Figs 15–17) ranges in length from 240–310 μm with a maximum width of 180–250 μm. All the dorsal setae are very long, simple and procumbent. Setae (*il*) and (*la*) are more or less equal in length and both pairs of setae reach the rostral bases. The sensilli are 40–55 μm long, lanceolate and serrated marginally. The exobothridial setae (*ex*) are moderately long. The *notogaster* (Figs 14, 18), 500–640 μm long and with a maximum depth of 300–460 μm, is rather globular in comparison with other species of the genus. All the setae are long (greater than the distance c_1–d_1), simple and almost erect. Seta c_1 is inserted on the posterior margin of the collar and setae c_{2-3} submarginally. Vestigial f_1 is located adjacent and just dorsal to the seta h_1, towards the mid-dorsal line. The fissures *ip* and *ips* are absent. On each *anal plate* there are five long setae; an_{1-2} and ad_3 being more or less equal in length and somewhat shorter than setae ad_{1-2}. The *chelicerae* are 170–190 μm long. The principal segment carries 12–26 sharply pointed spines on the paraxial surface and 22–25 conical spines antiaxially. The *leg chaetotaxy* is of the 'complete type' and on femur I (Fig. 8) the dorsal seta is long (equal in length to *l'*), slightly curved and covered in whorls of blunt serrations.

MATERIAL: Two specimens from litter under 'broom (*Genista*)' [= *Sarothamnus*] growing under willows, Burgweinting, Regensburg, 16.viii.1959 (M. Sellnick), deposited in the collections of the Zoological Museum of the University of Hamburg. One of these specimens (A31/80) from sample no. 59059 is hereby designated as the ***neotype***. A further ten specimens were examined from rotten wood and litter beside a brooklet (sample no. 61 R45), Donaustaufer Forest, Regensburg, 27.vi.1961 (L. van der Hammen) (RNH, Leiden). *P. globosus* was always recorded in small numbers in the Regensburg samples examined.

REMARKS: *P. globosus* is a very distinctive species being characterized by the 'globular' form of the notogaster. In comparison with German specimens, it was found that the British material examined was considerably larger (notogastral length 570–850 μm) and more heavily sclerotized. It is interesting that Jacot did not regard *globosus* as a *Phthiracarus* species, but rather as the male of *Hoplophora decumana* (= *Oribotritia decumana*).

Phthiracarus laevigatus (C. L. Koch)

Hoplophora laevigata Koch, 1844 : Heft. 38, t. 16. Regensburg [type series presumed lost].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Figs 14–18 *Phthiracarus globosus*: (14) notogaster, lateral; (15) aspis, dorsal; (16) sensillus; (17) aspis, lateral; (18) notogaster, dorsal.

Phthiracarus laevigatus: Jacot, 1936 : 167; van der Hammen, 1963 : 704. NEOTYPE (designated), Donaustaufer Forest, Regensburg (RNH, Leiden) [examined].

This species has been adequately redescribed by van der Hammen (1963).

Phthiracarus lentulus (C. L. Koch)

(Figs 19–24)

Hoplophora lentula Koch, 1841 : Heft. 32, t. 16. Regensburg [type series presumed lost]. NEOTYPE (here designated), Taimering, Regensburg (RNH, Leiden, P2001–4).

Phthiracarus lentulus: Jacot, 1936 : 175 [in part]. Topotypes, Unter-Isling/Burgweinting, Regensburg (MHN, Geneva, 3135h) [examined]. [*Phthiracarus lentulus*: Feider & Suciu, 1957 : 5. Misidentification.]

ADULT: Medium-sized. The *aspis* (Figs 21–23) ranges in length from 270–310 μm with a maximum width of 220–240 μm. Setae (*il*) and (*la*) are about equal in length and both pairs of setae extend half the distance *il-ro*. The rostral setae (*ro*) reach the anterior aspal margin. The sensilli are 70–90 μm in length and slender; proximally the sensillar margin is smooth while the distal part is serrated. The exobothridial setae (*ex*) are moderately long. The *notogaster* (Figs 19–20) ranges in length from 500–580 μm with a greatest depth of 400–440 μm. All the setae are short (less than c_1–d_1), stout and more or less erect. Seta c_3 is located on the posterior collar margin and setae c_{1-2} submarginally. Vestigial f_1 is located anterior to the seta h_1 while the fissures *ip* and *ips* are absent. On each *anal plate* there are three setae (ad_{1-2} vestigial); setae an_{1-2} being slightly longer than ad_3. The *chelicerae* are 190–200 μm long with 18–26 sharply pointed spines on the paraxial surface of the principal segment and 17–35 conical spines antiaxially. The *leg chaetotaxy* is of the 'complete type', the solenidia being long and almost straight. On tarsus I the distal seta coupled with solenidion ω_2 is long and divided into two parts by a longitudinal constriction. On femur I (Fig. 24) setae *d*, (*v*) and *l′* are all located at about the same level on the segment. Seta *d*, which is almost as long as *l′*, is thickened, curved and bluntly serrated.

MATERIAL: Four specimens from moist wood, moss and litter, Taimering, Regensburg, 19.vi.1961 (L. van der Hammen), deposited in the collections of the Rijksmuseum van Natuurlijke Historie, Leiden. One of these specimens (P2001–4) is hereby designated as the ***neotype***.

REMARKS: Koch recorded *lentula* predominantly in moss in woods and described the species as being of medium size with short notogastral setae. It is evident that the sensilli were probably either short or very fine, since these were not included by Koch in his original figure. The sensilli are indeed very fine in *lentulus* (Fig. 23), a feature which was also noted by Jacot in his redescription of this species.

Phthiracarus longulus (C. L. Koch)

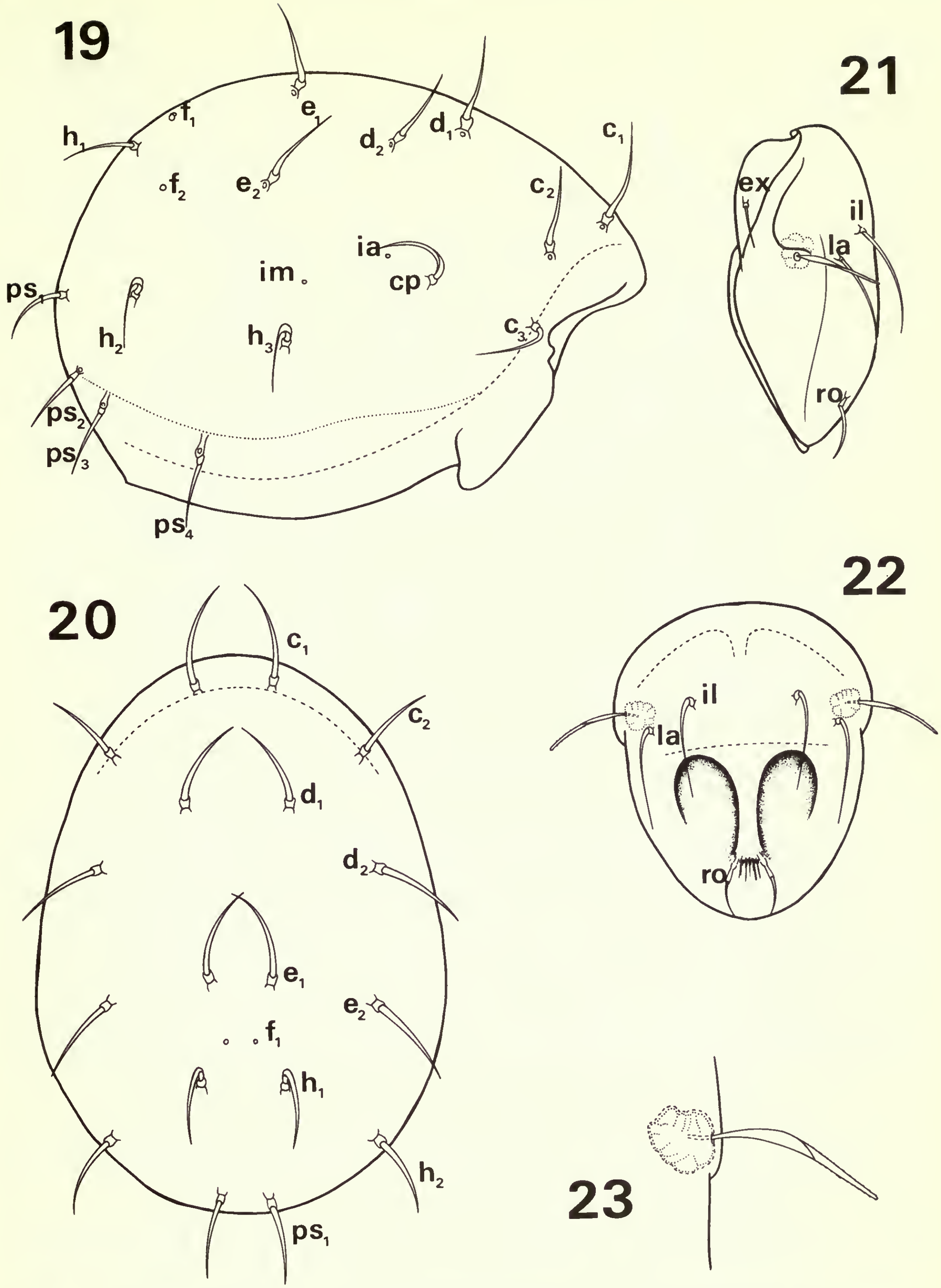
(Figs 25–31)

Hoplophora longula Koch, 1841 : Heft. 32, t. 17. Schweighauser Forest, Regensburg [type series presumed lost]. NEOTYPE (here designated), Donaustaufer Forest, Regensburg (RNH, Leiden, P2012–15).

Phthiracarus ferrugineus (Koch) *sensu* Jacot, 1936 : 179 [in part]. Topotypes, Dechbetten Forest, Regensburg (MHN, Geneva, 3119h) [examined].

Phthiracarus tardus Forsslund, 1956 : 216. Holotype, Västerbotten, Sweden (paratype, BMNH, London, 1964.7.13.78) [examined]. **Syn. nov.**

ADULT: Small and weakly sclerotized. The *aspis* (Figs 27, 29–30) ranges in length from 220–255 μm with a maximum width of 170–190 μm. The interlamellar setae (*il*) which are inserted on a level with the bothridia, are twice as long as the lamellars (*la*) and extend almost to the rostral bases (*ro*). The sensilli are lanceolate, serrated marginally, and range in length from 30–40 μm. The exobothridial setae (*ex*) are short. The *notogaster* (Figs 26, 28) is somewhat elongate and ranges in length from 430–490 μm with a maximum depth of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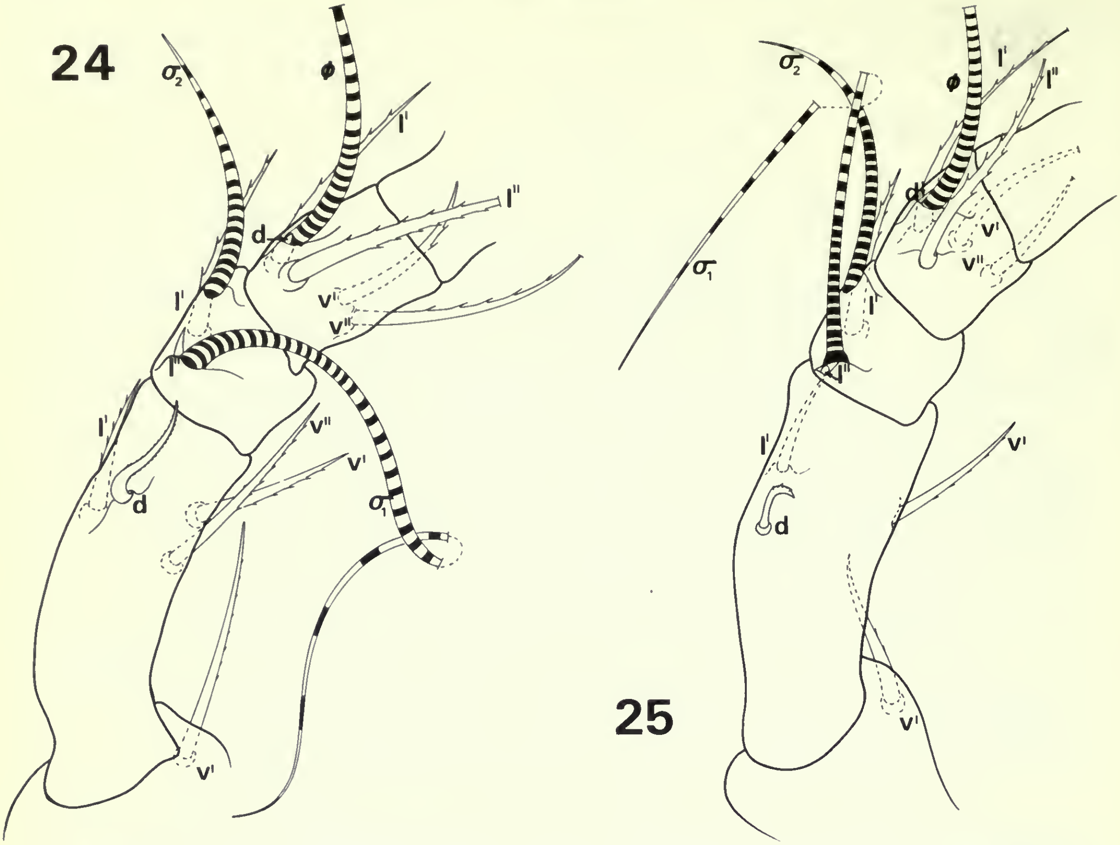
Figs 19–23 *Phthiracarus lentulus*: (19) notogaster, lateral; (20) notogaster, dorsal; (21) aspis, lateral; (22) aspis, dorsal; (23) sensillus.



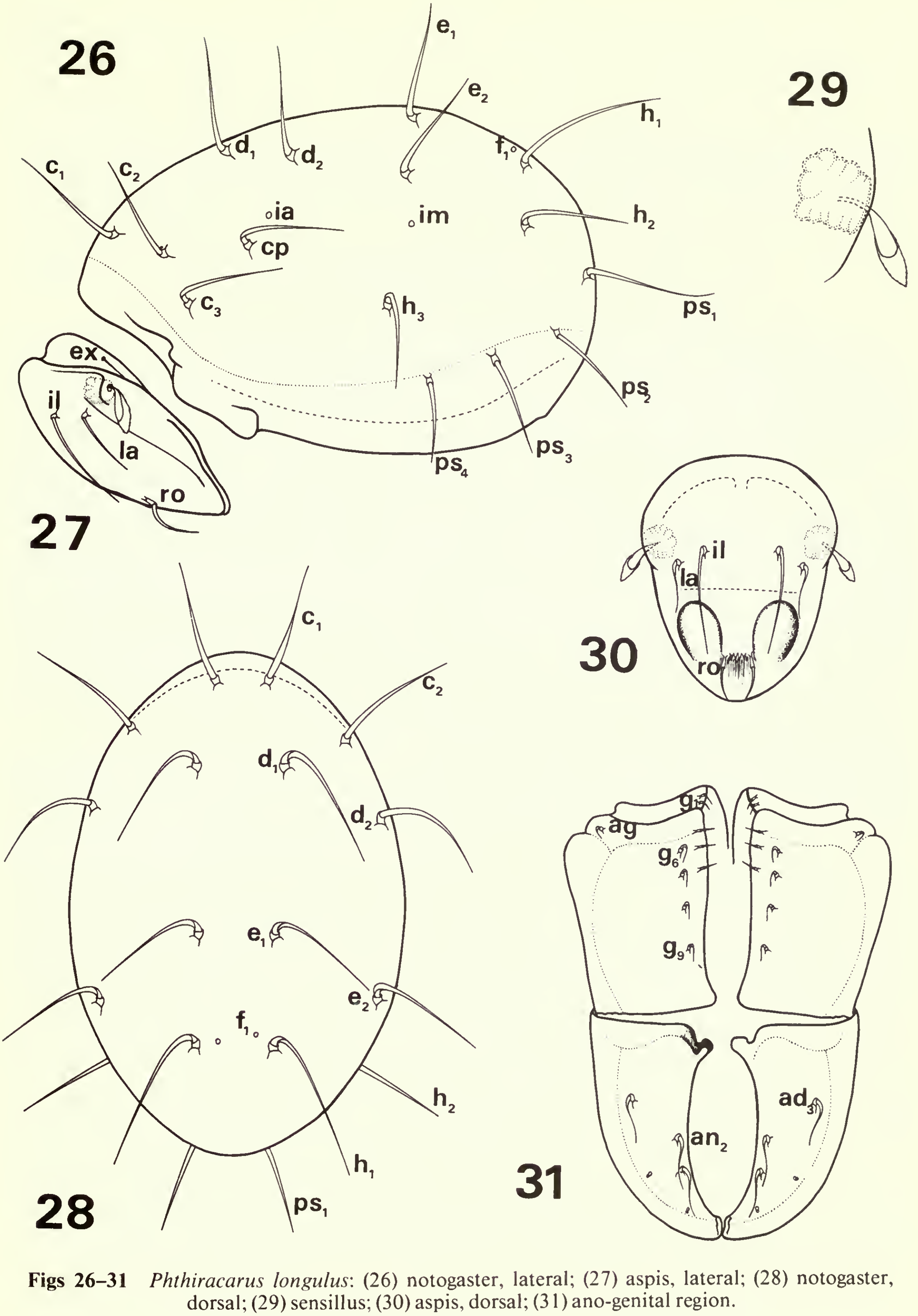
Figs 24–25 Leg I, trochanter to tibia, posterolateral aspect: (24) *Phthiracarus lentulus*; (25) *Phthiracarus longulus.*

300–320 μm. All the setae are erect and more or less equal to the distance c_1–d_1. Setae c_{1-3} form a row immediately behind the posterior collar margin while vestigial f_1 is located just dorsal to the seta h_1 and towards the mid-dorsal line. The fissures *ip* and *ips* are absent. On each *anal plate* (Fig. 31) there are three rather short setae, ad_3 being the shortest. The *chelicerae* are 150–200 μm long with 4–14 sharply pointed spines on the paraxial surface of the principal segment and 6–10 conical spines antiaxially. The *leg chaetotaxy* is of the 'reduced type' (see Parry, 1979) with three setae on femur I (*v′* absent) and no setae on genu IV (*l′* absent). Tarsus II bears 12 setae (subunguinial seta present), a feature which is generally associated with 'complete chaetotaxy' species. All the solenidia are moderately long and straight. Solenidion ω_2 on tarsus I is coupled with a minute distal seta. On femur I (Fig. 25) the dorsal seta is short, serrated, curved distally and located posterior to the setae *l′* and *v′*.

MATERIAL: Eight specimens from rotten wood and litter beside a brooklet, Donaustaufer Forest, Regensburg, 27.vi.1961 (L. van der Hammen), deposited in the collections of the Rijksmuseum van Natuurlijke Historie, Leiden. One of these specimens (P2012–15) from sample no. 61 R45 is hereby designated as the ***neotype***.

REMARKS: Koch recorded *longula* in moss in woods, a species he described as being small with long, fine notogastral setae and rather short, round-ended sensilli.

Of the species here described, *P. longulus* appears to be the most abundant in all the Regensburg samples. The species has been recorded only rarely in the British Isles but in Sweden the author has found it to be extremely widespread.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Figs 26–31 *Phthiracarus longulus*: (26) notogaster, lateral; (27) aspis, lateral; (28) notogaster, dorsal; (29) sensillus; (30) aspis, dorsal; (31) ano-genital region.

Survey

Of the eight *Phthiracarus* species described by C. L. Koch, six are capable of being reidentified with reasonable certainty. The two remaining species (*lucida* and *straminea*) cannot in the author's opinion be separated by any morphological characters mentioned in the original descriptions, although *lucida* was collected from a 'swampy' meadow, while *straminea* was recorded from moss in woods. However, *Phthiracarus* species are not generally considered to be habitat specific and it seems likely therefore, that Koch was in fact concerned with only one species, different specimens of which exhibited minor differences in colour.

Acknowledgements

The present study was based largely on specimens kindly sent by Dr L. van der Hammen, Rijksmuseum van Natuurlijke Historie (RNH), Leiden. Specimens from the Jacot and Sellnick Collections were examined through the courtesy of Dr B. Hauser, Muséum d'Histoire Naturelle (MHN), Geneva, and Dr G. Rack, Zoologisches Institut und Zoologisches Museum (ZM), Hamburg.

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The status of *Lamingtona lophorhina* McKean & Calaby, 1968 (Chiroptera: Vespertilionidae)

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Introduction

The genus *Lamingtona* and its sole species *L. lophorhina* were described by McKean & Calaby (1968) on the basis of six specimens from Mount Lamington in Northern Province, eastern Papua New Guinea, at 8° 55′ S, 148° 10′ E. Although showing *Lamingtona* to have a clear relationship to *Nyctophilus*, the original account is insufficiently detailed to permit a proper assessment of its status or of possible relationships of *L. lophorhina* to any of the several currently recognized species of this predominantly Austro-Papuan genus. The original material of *L. lophorhina* is housed in the South Australian Museum, Adelaide and in the collections of the Commonwealth Scientific and Industrial Research Organisation (Division of Wildlife Research), Canberra. Through the courtesy of Dr J. H. Calaby we have been able to examine the two paratypes from Canberra and to compare them directly with most of the described forms of *Nyctophilus*, with especial attention to those already known from New Guinea.

Systematic Section

McKean & Calaby (1968) compared *Lamingtona* primarily with *Nyctophilus*, although only two species (*timoriensis* and *geoffroyi*) of the latter are actually mentioned in their account. The principal diagnostic character that they use in separating *Lamingtona* from *Nyctophilus* and from its close relative *Pharotis* is the absence in *Lamingtona* of any band of integument connecting the ears across the forehead and they also remark that the ears of *Lamingtona* are smaller and the tragus not broadened basally as it is in these genera. In *Nyctophilus* it has been possible to examine specimens in alcohol of *geoffroyi, timoriensis, gouldi, bifax, walkeri, microdon, arnhemensis* and *microtis* (the last including *bicolor*), the species that tentatively we recognize in this genus, and in *Pharotis* similar examples of its sole representative, *P. imogene*. The ears are connected by a moderate or high band (which incidentally is not an extension of their inner or medial margins, but a separate structure arising from the outer or medial surface of each conch) in *Pharotis imogene* and in all of the species of *Nyctophilus* except *arnhemensis* and *microtis*. In *arnhemensis* the band is low and in *microtis* only slightly developed and barely discernible or absent in the midline, a point made clear in the original description of this species by Thomas (1888) who says 'band across the forehead nearly or quite obsolete in the centre'. On occasion, therefore, the ears are not joined at all. In *Pharotis imogene* and in several of the species of *Nyctophilus* the ears are large or sometimes very large, but those of *N. microtis* are relatively small, as its name implies, although Thomas (1915) found them to be rather larger than he thought originally (1888). The ears of *walkeri* and *arnhemensis* are of similar size or are only a little larger than

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those of *microtis*, which in turn resemble the ears of *Lamingtona* in size. The tragus is broadened basally in all except *Nyctophilus microtis*, although the extent of such widening may be slight. In *microtis*, however, this broadening of the tragus is often very poorly marked and may be virtually absent.

According to McKean & Calaby (1968) *Lamingtona lophorhina* lacks an ear band. Examination of the two paratypes (♀♀ CM 2090, 2091) shows this to be correct in the sense that the ears are not joined near the bases of their inner or medial margins by an obvious band of integument. However, although in both paratypes the area between and in front of the ears is densely pilose, careful investigation reveals the presence of a low integumentary ridge in the dry skins, extending from a point just behind the inner margin of each ear towards the midline. These ridges do not quite reach the median line but diminish in height towards the centre of the head. The condition exactly resembles that found in *Nyctophilus microtis* in which the ears are supported medially by a thick, tapered integumentary ridge whose outer and highest parts are integral with the medial faces of the ears. As in the paratypes of *Lamingtona lophorhina* the integumentary ridges taper to the midline, which on occasion they do not quite reach, and at best the ears are joined medianly only by a low elevation. So far as can be determined from the dry skins the tragus in one paratype (CM 2091) is more or less spatulate and little widened basally but in the other example (CM 2090) the tragus is slightly widened in its lower part: in both the tragus has a bluntly rounded tip, inclined anteriorly and is closely similar to the tragus of *Nyctophilus microtis*. We can see no reason that supports the recognition of *Lamingtona* as a genus distinct from *Nyctophilus* on account of the characters originally proposed. Miller (1907) in defining *Nyctophilus* noted 'Ears . . . usually joined across forehead by a conspicuous band of membrane, but this obsolete at middle in one species . . .'. [Since Miller stated that he had examined *timoriensis, microtis* and *walkeri*, the 'one species' was presumably *microtis*.] Moreover, the extent of joining of the ears (and the shape of the tragus) is known to vary within other bat genera and scarcely justifies even subgeneric recognition, especially since in *Nyctophilus* the relatively rudimentary integumentary ridges of *microtis* and *lophorhina* are linked by the low band of *arnhemensis* to the higher, more obvious connecting bands of species of similar size such as *bifax, walkeri* and *microdon*. There appear to be no significant cranial features to support the subgeneric separation of *microtis* and *lophorhina* (and possibly *arnhemensis*) from the remaining species currently recognized in *Nyctophilus*.

In discussing the affinities of *Lamingtona* McKean & Calaby (1968) remarked that it 'probably belongs in the subfamily Nyctophilinae but because of the ear characteristics it falls outside that subfamily as currently defined'. This claim deserves examination, especially in view of the close correspondence between the ear of *L. lophorhina* and that of *Nyctophilus microtis*, even to the shape and size of the small internal lobe near the base of its posterior or outer margin. Although Tate (1941) did indeed mention 'large united ears' as one of several features of the subfamily, the original definition by Miller (1907) characterized it externally by the form and structure of the muzzle and noseleaf, without reference to the ears. Miller remarked that the subfamily 'Differs from the Vespertilioninae in the abruptly truncate muzzle, on the anterior face of which the nostrils open forward beneath a distinct horseshoe-shaped ridge or small noseleaf'. Incidentally, though the New World genus *Antrozous* (usually, though perhaps erroneously placed in the Nyctophilinae) has an ear band basically similar to that of *Nyctophilus*, it is interrupted in the middle, as on occasion is the rudimentary band of *N. microtis*, and therefore does not (contra Tate) join the two ears together. There are evidently no grounds for excluding *lophorhina* and *microtis* from the Nyctophilinae unless it is proposed radically to redefine this alleged subfamily. As pointed out by McKean & Calaby, *lophorhina* has the small noseleaf and grooved muzzle characteristic of *Nyctophilus*: in fact, so far as can be determined from the dry skins of the paratypes, it is very similar in rhinarial structure to *microtis*, with an apparently truncate muzzle.

The two paratypes (CM 2090, 2091) are dorsally a rather uniform reddish brown, ventrally a little paler and more ochreous: the wing membranes are blackish brown, the tail membrane brownish. Both have every indication of prolonged immersion in alcohol (from

1929 to 1967 according to McKean & Calaby, 1968): the dorsal pelage is blackish brown at the base but otherwise bleached reddish brown, the ventral pelage similarly coloured but with the tips of the hairs more ochreous or buffy brown. In general the pelage is dense and long both above and below, almost shaggy. It is noticeably long and thick on the head as far anteriorly as a line just anterior to the eyes: the muzzle and the anterior part of the underside of the chin are sparsely covered with shorter hairs. A similar distribution of fur on the head is found in *Nyctophilus microtis.*

So far as can be determined, the narial foliations of *lophorhina* consist of a raised ridge surmounting the nostrils, the second low ridge lying behind it divided medianly. A similar structure (type 2 of Thomas, 1915) characterizes *Nyctophilus microtis.* The ears closely resemble those of this species, and are moderate and full, with a rounded tip, the posterior margin of the ear evidently concave above the antitragal lobe. The basal third to one half of the medial surface of the conch is sparsely pilose as in *N. microtis.* As already discussed, the interaural band in the paratypes exactly resembles the rudimentary band found in that species, and both *lophorhina* and *microtis* have an essentially similar tragus.

The skull of *lophorhina* closely resembles that of *Nyctophilus microtis* in both size and structure. The sagittal crest in the two paratypes examined (one, CM 2091 with slightly worn teeth), however, is less developed frontally than in adults of *N. microtis*. The upper surface of the rostrum also provides a point of variation: in CM 2090 the rostrum has a very shallow, almost imperceptible median depression, while CM 2091 has a relatively deep, well-defined longitudinal sulcus. Mr Peter Aitken of the South Australian Museum has examined the holotype (M6404) and two of the remaining paratypes (M6402, M6403): the final paratype (M6401) is in alcohol with the skull *in situ*. He reports that M6402 has a relatively shallower, more saucer-shaped depression on the top of the rostrum than M6403 and M6404, which each have a very distinct, deep longitudinal rostral depression forming a more obvious trough.

There is a similar range of variation among the specimens representing *Nyctophilus microtis* and those referred to this species that we have examined, all from Papua New Guinea. The young adult holotype of *bicolor* (=*N. microtis bicolor*) (BM(NH) 5.11.28.2) from an unknown locality near the coast on the Aroa River, c. 9° 05′ S, 146° 48′ E has a dorsally flattened rostrum with no more than the slightest suggestion of any median depression, while another immature (AMNH 108531) from Sogeri, 9° 30′ S, 147° 33′ E, the type locality of *microtis* itself, has such a depression only faintly indicated. The holotype of *microtis* (BM(NH) 88.4.14.1) has a very shallow rostral depression much like that of CM 2090. A further specimen (BM(NH) 88.4.14.5) from Sogeri has a moderate longitudinal rostral depression similar to that of CM 2091 but shallower, while an example (BM(NH) 34.1.14.7) from Kokoda, 8° 53′ S, 147° 44′ E has a large, very deep median sulcus that is more greatly developed than the sulcus of this paratype of *lophorhina*. This last locality, incidentally, is but little distant from Mount Lamington at 8° 55′ S, 148° 10′ E, whence the original series of *lophorhina* was obtained. The collection of the American Museum of Natural History also includes a further six specimens from a variety of localities in Papua New Guinea that reflect this variation in the degree of development of the rostral depression. From the limited material available to us it does not seem to be correlated with geography, sex or with age (judged by tooth wear) once full maturity is achieved: the only specimens in which the rostral depression is virtually absent are clearly immature or young.

In size *lophorhina* almost exactly resembles *Nyctophilus microtis.* Ranges of selected measurements of *lophorhina* (from McKean & Calaby, 1968), followed by those of adults of *N. microtis* in the British Museum (Natural History) and in the American Museum of Natural History (number of specimens examined in parentheses): length of forearm 39–40 (6), 37·5–40·5 (8); length of ear 15–19·5 (6), 15–19 (7); condylobasal length 13·8–14·7 (5), 13·5–14·5 (5); length of maxillary toothrow (c–m^3) 5·3–6·0 (5), 5·5–6·4 (8).

Although small, the sample of specimens that we have examined leaves little doubt that *lophorhina* and *microtis* are conspecific, if indeed not synonymous, and also closely related to *bicolor*. However, the close proximity in eastern Papua of the type localities of these three forms and the paucity of material from this area makes any further evaluation of their taxonomic validity difficult if not impossible. The differences between such specimens as we have seen are small and indicate that at best only subspecific separation can be justified. For the present, therefore, we are inclined to accept only a single species, *Nyctophilus microtis*, with the provisional recognition of three subspecies, *N. m. microtis* Thomas, 1888, *N. m. bicolor* Thomas, 1915 and *N. m. lophorhina* McKean & Calaby, 1968.

Summary

A review of the characters ascribed to the vespertilionid genus *Lamingtona* McKean & Calaby, 1968 from New Guinea shows that it cannot be separated generically from the predominantly Austro-Papuan genus *Nyctophilus* and that there is no justification for its retention as a valid subgenus within *Nyctophilus*. Examination of paratypes of its type species *L. lophorhina* McKean & Calaby, 1968 together with further information from the original series indicates that it is conspecific and possibly synonymous with *Nyctophilus microtis* Thomas, 1888. Three subspecies of *N. microtis (N. m. microtis, N. m. bicolor* Thomas, 1915, *N. m. lophorhina* McKean & Calaby, 1968) are tentatively recognized in eastern Papua but lack of adequate material prevents any proper assessment of their valdity.

Acknowledgements

Our thanks are due to Dr J. H. Calaby, of the Division of Wildlife Research, Commonwealth Scientific and Industrial Research Organisation, Canberra, Australia who made possible an examination of part of the original series of *Lamingtona lophorhina*, and to Mr Peter Aitken, Senior Curator at the South Australian Museum, Adelaide, Australia who examined the holotype and other relevant paratypes on our behalf.

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The status of *Hipposideros galeritus* Cantor, 1846 and *Hipposideros cervinus* (Gould, 1854) (Chiroptera: Hipposideridae).

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Introduction

Considerable taxonomic confusion has surrounded the small leaf-nosed bats of Indo-Australia allied to *Hipposideros galeritus* Cantor, 1846 from Penang Island, and numerous names have been proposed since that date for specimens or populations from this extensive region. Suggested classifications have varied from the recognition of three or more species to the definition of no more than one, the grouping of the various named forms changing accordingly. However it has long been apparent that the Bornean population of these bats seemed critical to any consideration of the groups of taxa as a whole, but for many years the relative lack of specimens from a variety of Bornean localities made critical assessment difficult. Moreover, this difficulty is compounded by much confusion in the literature.

This study was initiated through the interest of the Earl of Cranbrook (formerly Lord Medway) who obtained specimens in Sarawak while with the Royal Geographical Society Expedition to Mount Mulu, 1977–1978. These although superficially referable to *H. galeritus*, on close examination seemed to represent two very similar but nevertheless distinct taxa. They have led to a further examination of specimens ascribed to *H. galeritus* or to its nominal allies in the collections of the British Museum (Natural History) and as a result it has proved possible to attempt some clarification of the status and relationships of the majority of the named forms previously associated in one way or another with this species. Representative material of a minority of described taxa or populations is either lacking or unavailable and to this extent our conclusions must remain provisional, although even so it has been possible to advance tentative opinions. At the same time we have endeavoured to indicate through detailed synonymies the wide variety of conflicting usages and differing opinions that exist in the literature of this relatively small group of bats, of which representatives are likely to be found in the majority of collections from Indo-Australia.

Material and Methods

One hundred and thirty-three specimens have been examined in the course of this study, all in the British Museum (Natural History) [BM(NH)]. For the most part they are identified by their registration numbers but a minority of specimens collected recently in southeastern Sulawesi has yet to be accessed and will be reported more fully in an account of the collection of which they form a part. By the courtesy of Dr C. Smeenk, we have also been able to borrow a series of critical specimens from the Rijksmuseum van Natuurlijke Historie, Leiden (RNH) which have proved very valuable. In addition, Professor J. D. Smith of California State University has generously provided measurements of a series of specimens that he obtained recently on the islands of the Bismarck Archipelago, off northeastern New Guinea. Qualitative assessments of external, cranial and dental characters are summarized in the systematic accounts. Measurements are in millimetres and were

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Bull. Br. Mus. nat. Hist. (Zool.) **41**(5): 279–294

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made entirely by one of us (P.D.J.) with dial calipers. In the text those relevant in diagnosis appear with the following abbreviations:

Length of forearm	FA
Length of 2nd phalanx of third and fifth digits	III^2, V^2
Length of tail	TL
Length of skull from canine to occipital condyle (condylocanine length)	CCL
Greatest width across zygomata	ZW
Greatest mastoid width	MW
Greatest diameter of tympanic annulus	TD
Crown width across third molars	M^3–M^3
Length of upper toothrow from canine to third molar inclusive	C–M^3
Width of third molar	M^3

Where series of specimens have been available the range of each measurement is given, preceeded in parentheses by the number examined and followed by the arithmetic mean, also in parentheses. Measurements of holotypes appear separately but are also included in the appropriate series.

History

Although *Hipposideros galeritus* Cantor, 1846 and *H. cervinus* (Gould, 1854) are in general use as the earliest identifiable names in this small complex of bats, it is possible that both may be antedated by *Rhinolophus crumeniferus* Lesueur & Petit, 1807 (pl. 35), from Timor Island. The status of this name has been reviewed and discussed by Tate (1941 : 367, footnote, 382, 387), Laurie & Hill (1954 : 56), Oey & Feen (1958 : 230), Hill (1963 : 23) and Goodwin (1979 : 79). It is based solely on a coloured plate and no holotype appears to exist. There is very little doubt that the bats depicted belong to the *galeritus* complex and although the plate is insufficiently detailed, they are probably referable either to *galeritus* or to *cervinus*. There are no subsequent records of bats referable to either of these from Timor and for the present the name is best left unallocated.

The taxonomic history of this small but involved grouping of bats thus begins with the description of *Hipposideros galeritus* Cantor, 1846 from Penang Island, Malaya, followed in quick succession by the recognition of *cervinus* Gould, 1854 from northern Australia, *labuanensis* Tomes, 1859 from Borneo, *longicauda* Peters, 1861 from Java and, rather later, of *brachyotus* Dobson, 1874 from India. Even at this early stage, considerable differences of opinion are apparent, Peters (1871) for example separating *galeritus* subgenerically from *labuanensis, cervinus* and *longicauda* but Dobson (1876, 1878) synonymizing *labuanensis, longicauda* and *brachyotus* into *galeritus* which, like *cervinus*, he considered a valid species. This author noted variations in the size of the noseleaf, tail length and wing insertion on the hindlimb in *H. galeritus* as he understood it, considering specimens of *labuanensis* and *brachyotus* intermediate between *longicauda* at one extreme and *galeritus* at the other. However, this variation is at least partially due to the fact that his *H. galeritus* is a composite of *H. galeritus* and *H. cervinus* as we define them, although not unexpectedly some of the features to which Dobson drew attention retain diagnostic significance. His association of *labuanensis* with *galeritus*, rather than with *cervinus*, has persisted until the present day and has led to many of the difficulties encountered in classifying this group of bats, since the majority of subsequent comparisons have been made against members of the Bornean population that *labuanensis* represents, rather than *galeritus* of which few specimens are known.

Five further names have been proposed since Dobson's studies: *batchianus* Matschie, 1901 from Batjan Island in the Molucca Islands, *schneideri* Thomas, 1904 from Sumatra, the posthumously published *misorensis* Peters, 1906 probably from Misor Island (= Schouten Island) off northeast New Guinea, *insolens* Lyon, 1911 from Borneo and finally *celebensis* Sody, 1936 from Sulawesi. Among these the account by Lyon of *insolens* marks an important point since this author found *insolens* and '*galeritus*' to occur sympatrically and thus demonstrated for the first time the existence of two distinct species in the Bornean population. Most later authors have endeavoured to recognize this in different ways but have been handicapped by the unavailability of type material, by a lack of specimens from critical areas or by reliance on the concept of *labuanensis* as representative of *H. galeritus*. On this last point for example, it seems clear from the measurements that they cite, that '*galeritus*' as understood by Lyon (1911), by Chasen (1931) when reporting specimens from Sabah or by Sody (1936) when using Bornean specimens for comparison is in fact the taxon that we recognize as *H. cervinus labuanensis. Hipposideros galeritus* and its allies have been listed, reviewed and discussed either entirely or in part by Chasen (1940), Tate (1941), Laurie & Hill (1954) and Hill (1963).

Chasen (1940) admitted weaknesses in his arrangement of the Malaysian members of the complex but correctly maintained two separate taxa in Borneo. He recognized two species, *H. longicauda* with *insolens* as its subspecies and *H. galeritus* with subspecies *labuanensis* and *schneideri*. Although he had at one time examined the holotype of *galeritus*, Chasen had no access to it when writing and took for comparison '*galeritus*' from Pahang which may well have been *H. cervinus labuanensis* as we understand it, leading him to associate *galeritus* with *labuanensis* and *schneideri*, rather than with *insolens* and *longicauda* which we have found to be its allies.

The first attempt at a cohesive review of the entire complex was made by Tate (1941) who presented much useful information and many useful characters for distinguishing the taxa. Unfortunately it is difficult to extract a coherent view of their classification from this rather confusing paper. The caption to the distribution map (p. 365) for the *galeritus* group provides one opinion with the recognition of four species: *H. galeritus* with subspecies *schneideri, H. longicauda, H. labuanensis* and *H. cervinus* with subspecies *insolens, celebensis* and *batchianus*. The text however (p. 367) offers a different view, Tate observing that for the sake of consistency with the then prevailing view that *galeritus* extends through Sumatra, Java and Borneo to Celebes, it must be further extended to include *cervinus* of New Guinea and Australia. He concludes that *brachyotus, labuanensis, insolens, celebensis, batchianus* and *cervinus* would be more or less valid subspecies of *galeritus*, with *schneideri* and *longicauda* as derived species. Later (p. 369) he reaffirms that *cervinus, batchianus, celebensis* and *insolens* are no doubt conspecific but remarks that *labuanensis* and *schneideri* are good species. Finally (p. 391) *labuanensis, celebensis* and *cervinus* (also on p. 392) are considered subspecies of *galeritus* but *insolens* and *schneideri* distinct species. Moreover (p. 391) he reports both *galeritus* and *schneideri* from North Pagi Island in the Mentawei Islands.

Tate (p. 367) also suggested that the holotype of *H. galeritus* consisted of a mismatched skin and skull, although apparently he only saw a photograph of the skull and had not examined the skin but instead relied upon Cantor's description. He considered that the skin had distinct affinities with *cervinus* but that the skull appeared to be that of a bat of the *bicolor* group. As a result he designated the skin as the type of Cantor's name. This opinion was accepted by Laurie & Hill (1954) and more particularly by Hill (1963) who concluded that the skull agreed closely with that of the cranially similar species *H. ater*, a member of his *bicolor* subgroup, otherwise readily distinguished from *H. galeritus* by the absence of lateral supplementary leaflets. Subsequent examination has shown clear cranial differences between *H. ater* and *H. galeritus* and with the advantage of additional specimens from Malaya and Thailand, that agree closely both externally and cranially with the holotype of *galeritus*, we have been able to establish that these assumptions are erroneous and that it is very unlikely that any mismatch has occurred.

Laurie & Hill (1954) endeavoured to reconcile the varying opinions advanced by Tate with the specimens then available in the British Museum (Natural History) although concerned chiefly with New Guinea and Sulawesi. These authors recognized two species, *H. galeritus* extending eastwards perhaps to Sulawesi, *H. cervinus* from Borneo to the Solomon Islands, with subspecies *insolens, celebensis* and *batchianus*. They considered the eastern *cervinus* to be slightly less specialized than the western *galeritus* and its allies and, although differing in detail, their concept has elements in common with that advanced in this paper.

Hill (1963) in reviewing the complex as a whole, adopted much of the treatment by Laurie & Hill and carried it further in uniting *galeritus* and *cervinus* into one species, *galeritus*, of which all other forms were made subspecies; *insolens* becoming a synonym of *labuanensis*, their differences being thought to reflect individual variation. This arrangement has been widely accepted but proves to be incorrect.

Systematic Section

The review by Hill (1963, p. 19) of the *galeritus* subgroup and (p. 52) of *H. galeritus* as this author understood it provides an account of the major external, cranial and dental features of bats here attributed to *H. galeritus* or *H. cervinus* but since it is based on a composite of both further definition is needed.

Hipposideros galeritus Cantor, 1846

Diagnosis and description. Antitragus subangular, tall, nearly one third of ear length in height; antitragal projection absent (a small antitragal fold towards rear of antitragus may suggest an antitragal projection but disappears when ear is flattened); internarial septum linear, slightly swollen (Fig. 1); upper margins of narial lappets slightly lobed; intermediate leaf simple, slightly inflated medianly, expanded laterally to form a small lappet on either side, nearly as wide or wider than posterior leaf; wing elements relatively long; tail long; generally five caudal vertebrae (exceptionally four or six); tail membrane large and extensive.

Skull with long braincase and short toothrow relative to condylocanine length (Fig. 2); rostrum inflated, in profile swollen above interorbital region which is very constricted and shortened anteroposteriorly, with an angular outline when viewed from above; zygomata slender with prominent, short, abruptly rising jugal process; greatest zygomatic width generally less or subequal to mastoid width; anterorbital foramen subtriangular to suboval;

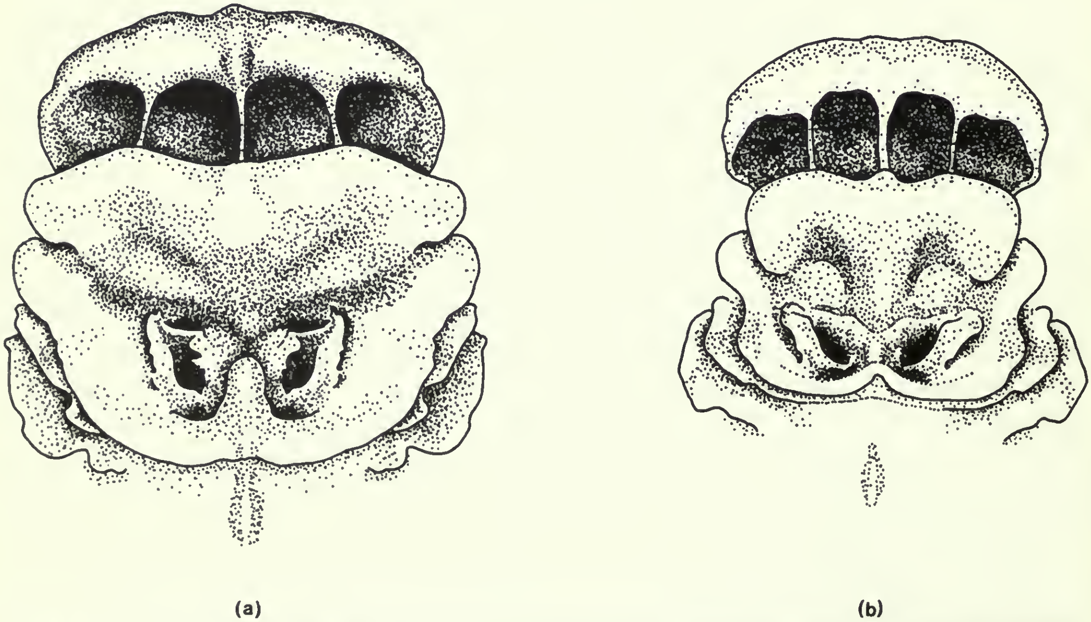

Fig. 1 Frontal view of noseleaf of: (a) *Hipposideros galeritus insolens*; (b) *Hipposideros cervinus labuanensis.*

braincase globose, frontal and parietal regions divided by a shallow depression; interparietal moderately swollen; mastoid well developed; post-palatal spicule obsolescent or absent; anterior sphenoidal ridges equal in length to posterior ridges to enclose a diamond-shaped sphenoidal depression; width of cochleae exceeding their distance apart, each one third concealed by a large tympanic annulus whose greatest diameter (2·70–3·00 [2·83]) is a little less than or approximately equal to the distance between the annuli across the sphenoidal

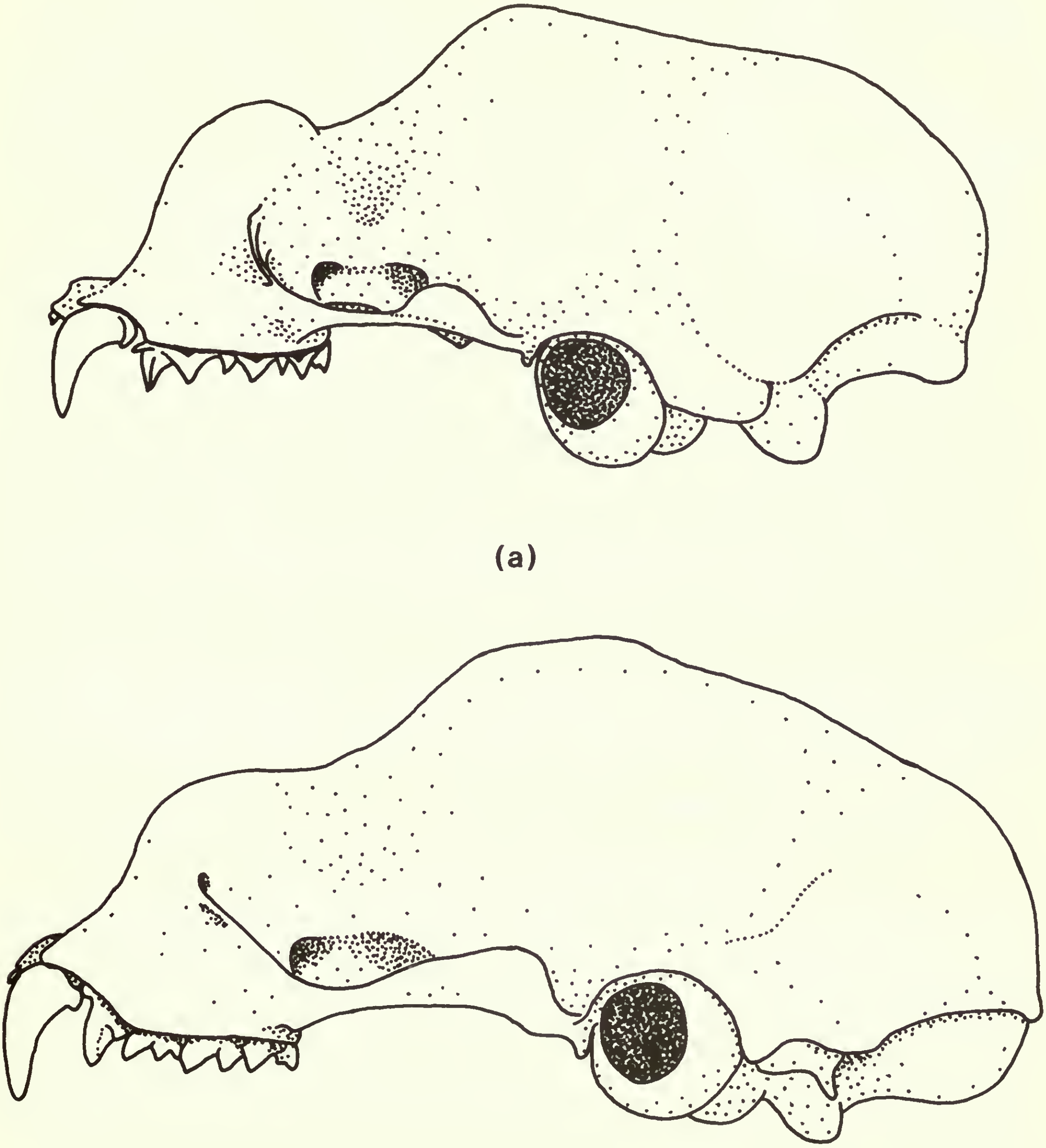

Fig. 2 Lateral view of the skull of: (a) *Hipposideros galeritus galeritus*; (b) *Hipposideros cervinus labuanensis*.

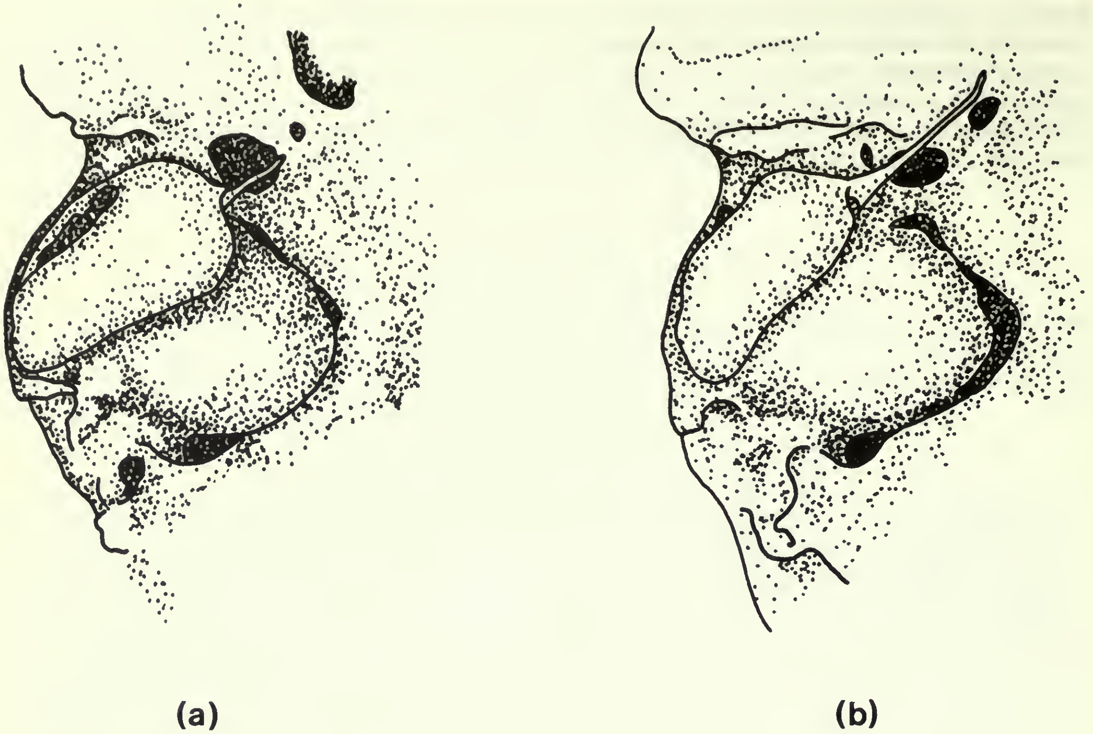

Fig. 3 Ventral view of external structure of right auditory region of skull of: (a) *Hipposideros galeritus insolens*; (b) *Hipposideros cervinus labuanensis.*

depression (except in *H. g. longicaudus* see discussion of this subspecies), annulus acutely angled to longitudinal axis of skull (Fig. 3); upper incisors bicuspid, outer lobes sometimes small; M^3 with well developed third commissure, fourth commissure small but evident; crown area of inner lower incisors less than crown area of outer pair.

DISTRIBUTION. India and Sri Lanka to Borneo and Java.

Hipposideros galeritus galeritus Cantor, 1846

Hipposideros galeritus Cantor, 1846 : 183 (Pinang [= Penang I.], Malaya); Lekagul & McNeely, 1977 : 167 (Satun Province, Thailand); Tate, 1941 : 367 (discussion, lectotype designated).
Rhinolophus (Phyllorrhina) galeritus, Wagner, 1855 : 659 (Pinang [= Penang I.], Malaya).
Phyllorrhina galerita, Fitzinger, 1870 : 885 (Malay Peninsula; Pinang [= Penang I.]).
Phyllorhina galerita, Peters, 1871 : 316 (Pinang [= Penang I.]); Dobson, 1876 : 69, 1878 : 141 (in part, Pinang [= Penang I.]).
Hipposideros galeritus galeritus, Chasen, 1940 : 46 (in part, Malay States); Tate, 1941 : 365 (mapped), 367 (type material discussed), 391 (N. Pagi, Mentawei Is.); Laurie & Hill, 1954 : 56 (in part, Penang, Malay States); Hill, 1963 : 53 (in part, Malay Peninsula); Medway, 1969 : 29, 1978 : 29 (in part, Penang I.).
Hipposideros galeritus group, Tate, 1941 : 358, 360, 364 (discussed).
[Hipposideros] galeritus, Tate, 1941 : 359 (listed), 369 (discussed), 384 (type material, further discussion).

HOLOTYPE. Adult ♂ BM(NH) 79.11.21.85. Slightly damaged skin, skull in good condition but left premaxilla and incisor missing, left zygoma broken, occipital region slightly damaged. Penang Island, Malaya. Originally in Indian Museum, Calcutta.

OTHER MATERIAL. MALAYA: ♀ BM(NH) 61.1718 (in alcohol, skull extracted) Bukit Kutu, Selangor, 1061 m; THAILAND ♂♀ BM(NH) 78.2351–2 (skins and skulls) Wang Bla Chan, Muang, Satun Province.

DIAGNOSIS. As species diagnosis and description; relatively small.

Measurements of holotype: FA 46·3; III^2 19·2; V^2 9·5; CCL 14·0; ZW 7·9; MW 8·9; TD 2·9; M^3–M^3 5·6; C–M^3 5·3; M^3 1·2.

Measurements of the series examined: FA (4) 39·0–48·1 (43·95); III^2 (4) 19·0–20·7 (19·80); V^2 (4) 9·5–10·7 (10·15); TL (3) 36·0, 40·0, doubtfully 49·0; CCL (4) 14·0–14·5 (14·30); ZW (4) 7·9–8·3 (8·15); MW (4) 8·3–8·9 (8·68); TD (4) 2·80–2·90 (2·88); M^3–M^3 (4) 5·5–5·7 (5·61); C–M^3 (4) 5·3–5·6 (5·46); M^3 (4) 1·20–1·35 (1·26).

REMARKS. Dobson (1876, 1878) evidently saw the holotype of *Hipposideros galeritus*, probably at the Indian Museum, Calcutta (it was presented to the British Museum (Natural History) in 1879) although (1876; 198) he does not list it from that collection. Since then it appears to have been commented upon only by Tate (1941) and Hill (1963).

Tate (1941) considered that the skin and skull of the holotype of *H. galeritus* were mismatched, although he had not examined the skin and apparently only had a photograph of the skull, and stated that the skin alone represented Cantor's type. However, the skull associated with this skin has an inflated rostrum, slender zygomata and U-shaped palation, all features distinguishing it from the *bicolor* subgroup, to which Tate and subsequently Hill (1963) thought it to belong and it is very similar to the skulls of other specimens of *H. galeritus*—as understood in this paper—from India, Sri Lanka, Thailand, Malaya and Borneo. In all, the zygomatic width is less than or subequal to the mastoid width, a feature otherwise characteristic of *H. bicolor* and its close allies. Tate also thought that the skin had affinities with *H. cervinus*. However, it has been possible to examine the ears and noseleaf in some detail after thorough soaking and there is clearly a tall, angular antitragus lacking any posterior antitragal projection, a prominent internarial septum and well developed, broad intermediate leaf, features which are characteristic of our concept of *galeritus* but not found in *cervinus*. Therefore there seems little to substantiate the contention that a mismatch of skin and skull has occurred and Tate's designation (p. 367) of the skin as the lectotype of *H. galeritus* should be discounted.

Lekagul & McNeely (1977) provided useful photographs of the noseleaf and skull, with notes on ecology and behaviour. However, those remarks extrapolated from Medway (1958) probably refer to *H. cervinus* (*H. c. labuanensis*) as understood here, rather than to *H. galeritus*.

DISTRIBUTION. MALAYA: Selangor; Penang Island. THAILAND: Satun Province.

Hipposideros galeritus brachyotus (Dobson, 1874)

Phyllorhina brachyota Dobson, 1874 : 237 (Central India).

Phyllorhina galerita, Dobson, 1876 : 69 (in part, Central India; Deccan).

Hipposideros galeritus, Blanford, 1888 : 287 (Indian Peninsula; Ceylon [=Sri Lanka]); Brosset, 1962 : 618 (Western and Central India: Chikalda; Ellora; Kanheri; Bombay; Bedsar Caves; Badomi).

Hipposideros brachyotus, Wroughton, 1913 : 36 (Kanara); 1915 : 85, 101 (Bihar; Ceylon [= Sri Lanka]; Ryley, 1914 : 689 (Gujerat); Phillips, 1923*a* : 274, 1923*b* : 155, 1924 : 25, 1935 : 94 (Ceylon [= Sri Lanka]).

[Hipposideros] brachyotus, Tate, 1941 : 358 (listed), 364 (mentioned), 369 (discussed), 381 (listed, holotype).

Hipposideros galeritus brachyotus, Tate, 1941 : 367 (discussion); Hill, 1963 : 54 (Ceylon [= Sri Lanka]; Mysore; Bombay; Bengal).

HOLOTYPE. Adult ♂ BM(NH) 9.1.4.70. In alcohol in fair condition, wing membranes damaged, skull extracted, in good condition, right upper incisor, left upper canine and left anterior upper premolar (PM^2) missing. Central India.

OTHER MATERIAL. INDIA: BM(NH) 75.11.3.3 (skin and skull) Lingasoogar, N.N.W. of

Bellary; ♂♀ BM(NH) 12.1.28.1–2 (in alcohol, skulls extracted) Konkan; ♂ BM(NH) 21.1.17.59 (skin and skull) Honawar, Kanara; ♂ BM(NH) 21.1.17.60 (skin and skull) Gaya, Bihar; ♀ BM(NH) 21.1.17.61 (skin and skull) Danta, Gujerat; SRI LANKA: ♂ BM(NH) 20.9.26.18 (skin and skull) Matugama; ♂♀ BM(NH) 21.1.17.57–58 (skins and skulls) Kala-Oya; BM(NH) 66.5525 (skin and skull) Dammeria, Passara, Uva.

Diagnosis. Similar in structure and size to *H. g. galeritus* but the material available is insufficient to assess its subspecific validity.

Measurements of holotype: FA 45·6; III^2 18·6; V^2 12·2; TL 35·6; CCL 14·2; ZW 8·6; MW 8·7; TD 2·70; M^3–M^3 5·8; C–M^3 5·4; M^3 1·45.

Measurements of the series examined: FA (10) 44·0–48·4 (46·05); III^2 (10) 18·3–21·6 (17·09); V^2 (10) 9·3–12·2 (10·97); TL (10) 30·0–37·5 (34·08); CCL (10) 14·1–15·4 (14·67); ZW (10) 8·4–9·1 (8·76); MW (10) 8·5–9·1 (8·79); TD (10) 2·70–3·00 (2·83); M^3–M^3 (10) 5·6–6·2 (5·88); C–M^3 (10) 5·3–5·9 (5·67); M^3 (10) 1·30–1·50 (1·43).

Remarks. This taxon has a relatively simple historical background, different authors considering it to be either specifically distinct or a subspecies of *H. galeritus*. Phillips (1923*a*, 1923*b*, 1924, 1935) provided notes on its behaviour, reproduction and ecology in Sri Lanka, Brosset (1962) gave similar comments on Indian populations and included a frontal photograph of the head. Both maintained that these bats have been observed only as isolates or in very small family groups, Brosset considering that they avoided other species. This is an interesting point that may reflect the fact that, in contrast to *H. cervinus, H. galeritus* is poorly represented in trapping samples and is comparatively rare in museum collections.

Distribution. INDIA: Gujerat; Mysore; Bihar. SRI LANKA.

Hipposideros galeritus insolens Lyon, 1911

Hipposideros insolens Lyon, 1911 : 129 (Upper Pasir River, southeastern Borneo); Chasen, 1931 : 112 (Baturong Caves, N. Borneo); Tate, 1941 : 391 (Perboewa, N.W. Borneo).
Hipposideros longicauda insolens, Chasen, 1940 : 46 (Borneo).
[Hipposideros] insolens, Tate, 1941 : 359 (listed), 368 (discussed), 384 (holotype).
Hipposideros cervinus insolens, Tate, 1941 : 365 (mapped); Laurie & Hill, 1954 : 56 (discussed).
Hipposideros galeritus insolens, Tate, 1941 : 367 (discussed), 369 (systematic status).
Hipposideros galeritus labuanensis, Davis, 1962 : 39 (in part?, Sandakan, Borneo); Hill, 1963 : 54 (in part, Borneo); Medway, 1965 : 57, 1977 : 51 (in part, Borneo).

Holotype. Adult ♂ USNM 154389. In alcohol, skull extracted, both in good condition (Poole & Schantz, 1942). Near Lowatsi, on the Upper Pasir River, southeastern Borneo. Not seen.

Other material. BORNEO: BM(NH) 0.7.29.4–7 (should be in alcohol but not found, skull only) Baram, Sarawak; 3♂ 4♀ BM(NH) 51.120–126 (in alcohol, skulls extracted) Long Lama Caves, Baram River, Sarawak; ♂♀ BM(NH) 59.150–1 (skins and skulls) Gua Bungoh, Bau, Sarawak; 3♀ BM(NH) 75.1896–8 (in alcohol) Niah Cave, Gunong Subis, 4th Division Sarawak; ♀ BM(NH) 78.123 (in alcohol) Gunong Mulu, Sarawak, 500 m; 3♂ 4♀ BM(NH) 78.2495–2501 (in alcohol) inland from Sangkulirang, mouth of River Baai, E. Kalimantan, 0° 59′ N, 117° 58′ E.

Diagnosis. Larger than *H. g. galeritus* or *H. g. brachyotus* with more robust skull; interorbital region longer and less angular in shape; upper incisor occasionally with reduced outer lobe.

Measurements of the series examined: FA (19) 45·7–52·2 (48·94); III^2 (19) 17·1–21·9 (19·46); V^2 (19) 10·1–13·2 (10·81); TL (19) 28·4–37·6 (33·81); CCL (4) 14·5–15·7 (14·90); ZW (7) 9·0–9·3 (9·10); MW (6) 8·8–9·2 (8·98); TD (7) 2·75–2·90 (2·85); M^3–M^3 (9) 6·1–6·6 (6·37); C–M^3 (7) 5·9–6·3 (6·19); M^3 (10) 1·50–1·70 (1·62).

Remarks. Lyon (1911) distinguished *H. insolens* from *H. galeritus* (clearly = *H. cervinus* *labuanensis* as understood here, from his measurements) by its distinctly longer forearm, tail and tibia, although he considered the skulls and dentition of the two taxa to be indistinguishable. Chasen (1931) also considered *insolens* a distinct species but later (1940) evidently revised this view and listed it as a subspecies of *H. longicauda* from Java. Despite the confusion of Tate's (1941) treatment of *insolens*, this author made an important contribution in distinguishing it from *labuanensis* and listing a number of cranial characters useful in separating the two taxa. This distinction was maintained by Laurie & Hill (1954) who regarded *insolens* as a subspecies of *H. cervinus* and *labuanensis* as a subspecies of *H. galeritus*.

More recently, Davis (1962) synonymized *insolens* and *labuanensis* but the measurements that he gave suggest that his sample consisted only of the latter and included no specimens referable to *insolens*. This view was followed by Hill (1963) who also synonymized *insolens* and *labuanensis* and further suggested that *insolens*, as understood by Lyon and Tate, might well refer to large individuals of *labuanensis*, the differences observed by Tate reflecting individual variation. However, although these features may be more variable than Tate thought, in combination with others listed above but not noted by Tate, they establish two species in Borneo, one represented by *H. galeritus insolens*, the other by *H. cervinus labuanensis.*

Distribution. BORNEO: Sarawak; Brunei; E. & S.E. Kalimantan.

Hipposideros galeritus longicaudus (Peters, 1861)

Phyllorhina longicauda Peters, 1861 : 708; 1871 : 321 (Surakarta, Java); 1906: pl. 5L, fig. 3 (head illustrated).
Phyllorhina galerita, Dobson, 1876 : 69; 1878 : 141 (in part, Java).
Hipposideros galerita longicauda, Sody, 1930 : 270 (C. Java).
Hipposideros longicauda longicauda, Chasen 1940 : 46 (Java)
[Hipposideros] longicauda, Tate, 1941 : 359 (listed), 369 (systematic status), 385 (holotype, remarks).
Hipposideros longicauda, Tate, 1941 : 365 (mapped), 367 (systematic status).
Hipposideros galeritus longicauda, Hill, 1963 : 56 (Java).

Holotype. Attempts to locate the holotype in the Museum für Naturkunde der Humboldt-Universität in Berlin (where it might be expected to be housed), the Forschungsinstitut und Natur-Museum Senckenberg, Frankfurt and the Staatliches Museum für Naturkunde, Stuttgart, have failed.

Other material. JAVA: ♂♀ RNH 15103–7, 15168–9, 15258, 15319, 15330 (skins and skulls) Panganderan, Central Java; ♂♀ RNH 15170, 15259 Toenggilis, West Java.

Diagnosis. This taxon is poorly known with few specimens or records. As species diagnosis but averaging slightly smaller than *H. g. galeritus* and *H. g. brachyotus*, considerably smaller than *H. g. insolens* and differing from all other subspecies in having small tympanic annuli (2·4–2·5[2·46]). The most noticeable feature is the long tail of the holotype, although Sody (1930) reported four specimens which have rather shorter tails. According to this author the skulls of these Javan examples are strikingly larger than those of the Sulawesian specimens that he subsequently described (1936) as *celebensis*, although the series that we have examined does not support this.

Measurements of the holotype: FA 48 (Peters, 1861), 48·3 (Dobson, 1876); TL 44 (Peters, 1861), 40·6 (Dobson, 1876), TL of four additional specimens 32–36 (Sody, 1930).

Measurements of the series examined (skin measurements taken from dried skins): FA (II) 45·3–48·0 (46·50); III^2 (II) 16·5–19·2 (17·76); V^2 (II) 9·5–11·4 (10·64); TL not measured because vertebrae have been removed from dried skins; CCL (II) 13·6–14·4 (13·93); ZW (II) 8·1–8·6 (8·29); MW (II) 8·3–8·8 (8·53); TD (II) 2·4–2·5 (2·46); M^3–M^3 (10) 5·4–5·8 (5·63); C–M^3 (II) 5·2–5·6 (5·45); M^3 (10) 1·3–1·45 (1·39).

Remarks. Peters (1861) and Dobson (1876) seem to have been the only authors who have made a direct examination of the original material. There are, however, excellent drawings of the head among the posthumously published drawings of Peters (1906) which, with the original account, establish *longicaudus* as a member of the *galeritus/cervinus* complex. It has a tall, subangular antitragus and large noseleaf, with prominent internarial septum and broad intermediate leaf, all features which with the long tail are characteristic of *H. galeritus*. A small projection illustrated towards the rear of the antitragus may be an antitragal projection similar to that of *H. cervinus* but may equally result from a fold in the ear membrane, disappearing when the ear is flattened. Such a fold is found in some individuals of *H. galeritus*. The illustration by Peters may not be based on the specimen measured in his original account, since he appears to have had more than one example. The frontal pit in males is described by Peters (1861) yet Dobson (1876) stated that he had examined the adult female type, indicating the existence of at least two specimens. Chasen (1940) and Tate (1941) regarded *H. longicauda* as a distinct species; Tate considered that it agreed with the *galeritus* group but was probably atypical.

Distribution. JAVA: central and west.

Hipposideros cervinus (Gould, 1854)

Diagnosis and description. As in *H. galeritus* but antitragus rounded, short, approximately one-eighth of ear length in height; an acutely pointed antitragal projection; internarial septum low, narrow, not swollen (Fig. 1); narial lappets well developed, not lobed; intermediate leaf slightly inflated dorsally, slightly expanded laterally, narrower than either anterior or posterior leaves; forearm, distal phalanges and tail not especially lengthened; usually four caudal vertebrae, sometimes five, rarely six.

Skull with short braincase and long toothrow relative to condylocanine length (Fig. 2); rostrum only slightly inflated, in profile normally level with interorbital region, with a rounded outline when viewed from above; zygomata with rather long, gradually sloping jugal process; zygomatic width greater than mastoid width; anterorbital foramen suboval to ellipsoidal; interparietal only slightly swollen; mastoid uninflated; a blunt median postpalatal spicule sometimes present; anterior sphenoidal ridges longer than posterior ridges to enclose a pyriform sphenoidal depression; cochleae only slightly wider than their distance apart; tympanic annulus overlaying less than one quarter of the cochlea; greatest diameter of annulus (2·05–2·65 [2·36]) one half to three quarters of the distance between the annuli across the sphenoidal depression; annulus shallowly angled to longitudinal axis of skull (Fig. 3); upper incisors small, at most only weakly bicuspid, with rounded inner lobe, outer lobe when present minute; M^3 slightly reduced, third commissure shortened; fourth commissure absent; crown area of inner lower incisor equal to or slightly less than crown area of outer tooth.

Distribution. Malaya, Sumatra and Phillippine Islands east to New Hebrides.

Hipposideros cervinus cervinus (Gould, 1854)

Rhinolophus ? cervinus Gould, 1854; pl. 34 (Cape York and Albany I., Australia).
Rhinolophus (Phyllorrhina) cervinus, Wagner, 1855 : 661 (Cape York and Albany I., Australia).
Phyllorrhina cervina, Fitzinger, 1870 : 873 (Cape York and Albany I., Australia); Peters, 1871 : 321 (in part, Cape York and Albany I., Australia; Aru I.).
Phyllorhina cervina, Dobson, 1878 : 142 (Cape York and Albany I., Australia; Aru Islands; Waigiou Island; New Guinea).
Hipposideros galerita galerita, Sody, 1930 : 267 (Mampoegrotto, S. Celebes [= Sulawesi]).
Hipposideros cervinus, Sanborn, 1931 : 24 (New Guinea: Marienberg; Santa Cruz Is.: Fenvaloa; New Hebrides: Espiritu Santo, Efate, Malo); Sanborn & Nicholson, 1950 : 331 (New Hebrides: Espiritu Santo).

Hipposideros celebensis Sody, 1936 : 47 (Mampoe Cave, S. Celebes [= Sulawesi]).

(?) *Hipposideros galeritus galeritus*. Shamel, 1940 : 354 (Peling [= Peleng] I.; Gimpoe or Bada, Celebes [= Sulawesi]).

[Hipposideros] cervinus, Tate, 1941 : 359 (listed), 368 (discussed, S. New Guinea: Fly R.; Aru I.; New Hebrides); 381 (holotype).

Hipposideros cervinus cervinus, Tate, 1941 : 365 (mapped), 369 (systematic status); Laurie & Hill, 1954 : 56 (New Guinea; Japen [= Jobi] I.; Kei Is.; Aru Is.; Trobriand Is.; Kiriwina; Bismarck Archipelago: New Ireland; Solomon Is., Guadalcanar, Bougainville); Hill, 1956 : 78 (Solomon Is.: Rennell); McKean, 1972 : 26 (New Guinea: Papua).

Hipposideros cervinus celebensis, Tate, 1941 : 365 (mapped); Laurie & Hill, 1954 : 57 (Celebes [= Sulawesi]).

Hipposideros galeritus cervinus, Tate, 1941 : 367 (discussed), 391 (New Guinea: W. Irian), 392 (variation); Hill, 1963 : 57 (New Guinea: Waigeo I.; Japen [= Jobi] I.; Kei Is.; Aru Is.; N. Australia; Bismarck Archipelago: New Ireland; Trobriand Is.: Kiriwina; Solomon Is.: Bougainville, Guadalcanar, Fauro, Russell, Rennell; Santa Cruz Is.: Vanikoro; New Hebrides: Espiritu Santo, Efate, Fenvaloa); Hill, 1971 : 574 (Solomon Is.: San Jorge I.).

[Hipposideros] celebensis, Tate, 1941 : 359 (listed), 368 (S. Celebes [= Sulawesi]), 381 (holotype).

Hipposideros galeritus celebensis, Tate, 1941 : 367 (discussed), 369 (systematic status), 391 (S.Celebes [= Sulawesi]); Hill, 1963 : 56 (Celebes [= Sulawesi]).

Hipposideros galeritus labuanensis, Laurie & Hill, 1954 : 56 (in part, ? extending to Celebes [= Sulawesi]).

Hipposideros galeritus, Koopman, 1979 : 9 (Karkar I., Crown I., off N.E. coast of New Guinea; Bismarck Archipelago: New Britain).

HOLOTYPE. Adult ♀ BM(NH) 55.11.7.13. Skin in good condition, rostrum and mandible of skull. Caves on Albany Island, Cape York, N. Australia.

OTHER MATERIAL. AUSTRALIA: BM(NH) 55.11.7.12. (skull), ♀ BM(NH) 7.1.1.304 (skin and skull), ♀ BM(NH) 26.3.11.203 (in alcohol) Cowal Creek, ♀ BM(NH) unregistered (in alcohol) Cape York; NEW HEBRIDES: 1♂ 3♀ BM(NH) 73.1361–4 (in alcohol, skulls extracted) Amok, Malekula Is., ♂♀ BM(NH) unregistered (in alcohol, skulls extracted) Espiritu Santo; SANTA CRUZ Is.: ♂ BM(NH) 55.359 (skull) Vanikoro; SOLOMON ISLANDS: 2♂ 1♀ BM(NH) 87.1.18.13–15 (in alcohol, skulls extracted) Fauro I, ♂ BM(NH) 88.1.5.27 (in alcohol, skull extracted) Aola, Guadalcanar, ♂♀ BM(NH) 33.11.11.3–4 (skins and skulls) Talena, Russell I., ♀ BM(NH) 54.883 (skin and skull) Rennell I., 11♂ 13♀ BM(NH) 67.2063–86 (in alcohol, skulls extracted) Talise, San Jorge I.; TROBRIAND ISLANDS: ♀ BM(NH) 96.10.5.11 (in alcohol, skull extracted) Kiriwina; BISMARCK ARCHIPELAGO: BM(NH) 77.7.18.12 (skin and skull) New Ireland; NEW GUINEA: BM(NH) 50.12.16.1–2,5 (skins and skulls), BM(NH) 86.11.3.7–8 (skins and skulls) Jobi I., 4♂ 2♀ BM(NH) 97.8.7.10–15 (in alcohol, skulls extracted) Haveri, BM(NH) 10.7.16.10 (skull) Arfak Mts., 8♂ 8♀ BM(NH) 33. 6.1.10–25 (in alcohol, skulls extracted), BM(NH) 69.325 (skin and skull) Javavere Caves, Papua, ♂♀ BM(NH) 69.326–7 (skins and skulls) E. of Port Moresby, Papua, 6♂ 8♀ BM(NH) 80.618–631 (in alcohol) Siboma, Morobe Province; ARU ISLAND: + 16♂ + 10♀ BM(NH) 10.3.2.4–37 (in alcohol and skins and skulls) Wasi; KEI ISLAND: ♂♀ BM(NH) 99.12.14.9–10 (in alcohol, skulls extracted); SULAWESI: 2♂ 3♀ BM(NH) unregistered (in alcohol, skulls extracted), paratypes of *H. celebensis* ♂♀ RNH 29297, 29303 (skins and skulls) Mampoe Grot, 20 km from Watoe Pone.

DIAGNOSIS. As species diagnosis and description. Variable in size but generally relatively small. Specimens from Sulawesi, Aru and Kei Islands have a blunt post-palatal spicule which is lacking in those from New Guinea, Cape York, Solomon Islands and New Hebrides.

Measurements of holotype: M^3–M^3 6·3; C–M^3 6·0; M^3 1·7.

Measurements of the series examined: FA (37) 40·4–48·2 (45·70); III^2 (37) 14·6–18·8 (16·81); V^2 (37) 8·7–11·1 (10·02); TL (37) 22·8–31·0 (27·16); CCL (25) 13·8–15·6 (14·44); ZW (26) 8·7–10·0 (9·18); MW (25) 8·2–9·2 (8·64); TD (24) 2·15–2·60 (2·29); M^3–M^3 (27) 5·7–7·0 (6·27); C–M^3 (27) 5·5–6·3 (5·91); M^3 (27) 1·4–1·7 (1·51).

REMARKS. Dobson (1878) distinguished *H. cervinus* from *H. galeritus*, with which he synonymized *labuanensis*, here regarded as a subspecies of *cervinus*. Among more recent authors, Tate (1941) provided comments on a number of specimens from New Guinea and remarked that two colour phases occurred, one red the other grey, and that there was some geographical variation in size. This author variously considered *cervinus* a valid species or a subspecies of *H. galeritus*. Laurie & Hill (1954) attempted to formalize the uncertainties of Tate's taxonomic treatment of *cervinus*, considering it a distinct species closely allied to *H. galeritus*.

Initially Sody (1930) referred Sulawesian specimens to *H. galeritus galeritus* but after comparison with specimens he thought represented Bornean *galeritus*, he decided (1936) that the Sulawesian specimens were specifically distinct, naming them *H. celebensis*. It is impossible to determine the identity of his comparative material from the measurements cited and it may have consisted of *H. cervinus labuanensis*, *H. galeritus insolens* or even a mixture of both. No morphological characters are described in either account. Some of the measurements given by Sody for *celebensis*, such as the length of the tail, the zygomatic and mastoid widths and the length of the upper toothrow are apparently comparable with those used in this study. However our measurements of two of the paratypes of *celebensis* conflict with those quoted by Sody, for instance the upper toothrow length which we find greater than given by Sody while the zygomatic and braincase breadths are less than his values. Since the two paratypes unquestionably belong to *H. cervinus*, agreeing closely with specimens of this species obtained recently in Sulawesi, it seems reasonable to assume that the entire series of *celebensis*, including the holotype, also belong to *H. cervinus*.

Shamel (1940) recorded specimens (in the National Museum of Natural History, Washington) from Sulawesi and Peleng Island as *H. galeritus galeritus* but gave no diagnostic information, although Tate later observed (1941 : 368) that the Peleng Island specimens exactly resembled *celebensis*. Tate stated that a series of specimens (in the American Museum of Natural History, New York) from S. Sulawesi, which he also referred to *celebensis*, agreed in most respects with *insolens* although smaller in size but approached *labuanensis* in a shorter M^3 with an incomplete cusp pattern. Tate allocated *celebensis* variously to *H. galeritus* (p. 367, 369, 391) or to *H. cervinus* (p. 365) and it is impossible from these remarks to decide to which species these specimens from Peleng Island and Sulawesi belong or if they are a mixture of both species. Only further examination will determine their status. Laurie & Hill (1954) treated *celebensis* as a subspecies of *H. cervinus* but suggested that the specimens recorded by Shamel seemed most likely to belong to *labuanensis* (which they considered to be a subspecies of *galeritus*), evidently assuming that two species occur on Sulawesi. Our investigations suggest that only one species, *H. cervinus cervinus*, occurs there.

DISTRIBUTION. The majority of islands and island groups from Sulawesi to the New Hebrides and North Australia.

Hipposideros cervinus labuanensis (Tomes, 1859)

Phyllorrhina labuanensis Tomes, 1859 : 537 (Labuan I. and Sarawak, Borneo).
Rhinophylla labuanensis, Gray, 1866 : 82 (no locality given).
Phyllorhina labuanensis, Peters, 1871 : 321 (Labuan I. and Sarawak, Borneo).
Phyllorhina galerita, Dobson, 1876 : 69, 1878 : 141 (in part, Labuan I., Borneo).
Hipposideros galeritus, Thomas, 1895 : 108 (Engano I., W. of Sumatra); Lyon, 1911 : 129 (Panebangan I., Pangkallahan River, upper Pasir River, Borneo).
Phyllorhina speoris, Jentink, 1897 : 52 (C. Borneo).
Hipposideros schneidersi (misprint = *schneideri*) Thomas, 1904 : 722 (Sukaranda, Sumatra); Tate, 1941 : 367, 369 (systematic status), 391 (N. Pagi I., Mentawei Is.).
Hipposideros galeritus galeritus. Chasen, 1931 : 111 (N. Borneo); Chasen, 1940 : 46 (in part, Malay States; Rhio [= Riouw] Archipelago; Banka I.; S. Natuna Is.); ? Sanborn, 1952; 104 (Mindanao I., Philippine Is.); Laurie & Hill, 1954 : 56 (in part, Malay States); Davis, 1961 : 90 (Malaya); Hill, 1963 : 53 (in part, Malay Peninsula; Riau [= Riouw] Archipelago; Banka; S. Natuna Is.); Medway, 1969 : 29, 1978 : 29 (in part, Malaya; Singapore I.).
Hipposideros galeritus labuanensis, Chasen, 1940 : 47 (Borneo); Tate, 1941 : 367 (systematic status),

391 (N.W. Borneo); Laurie & Hill, 1954 : 56 (in part, Borneo); Davis, 1962 : 39 (Borneo); Hill, 1963 : 54 (in part, Borneo; Labuan I.; Mindanao I. Philippine Is.); Medway, 1965 : 57, 1977 : 51 (in part, Borneo).

Hipposideros galeritus schneideri, Chasen, 1940 : 47 (Sumatra; ? Engano I.); Tate, 1941 : 365 (mapped); Hill, 1963 : 54 (Sumatra; Engano I.; Sipora I.; N. Pagi, Mentawei Is.).

[Hipposideros] labuanensis, Tate, 1941 : 359 (listed), 368 (discussed), 385 (holotype).

[Hipposideros] schneideri, Tate, 1941 : 359 (listed), 368 (discussed; Sumatra, Pagi), 389 (holotype).

Hipposideros labuanensis, Tate, 1941 : 365 (mapped), 369 (systematic status).

HOLOTYPE. Adult BM(NH) 7.1.1.305. Skin in good condition, skull lacking premaxillae, cranium damaged. Labuan Island, Borneo.

OTHER MATERIAL. BORNEO: 4♂ 3♀ BM(NH) 47.3.4.7–14 (in alcohol, skulls extracted), ♂♂ ♀♀ BM(NH) 56.9.19.4, BM(NH) 7.1.1.306, BM(NH) 11.1.18.6, BM(NH) 61.1046–9 (skins and skulls) Sarawak, ♂♂ ♀♀ BM(NH) 91.2.3.2, BM(NH) 0.7.29.6–7c, BM(NH) 4.8.6.1, BM(NH) 8.1.27.29–30 (in alcohol and skins and skulls) Baram, Sarawak, 2♂ BM(NH) 95.11.5.2–3, 6♂ BM(NH) 8.1.27.36–41, 2♂ 1♀ BM(NH) 59.157–9, 3♂ 6♀ BM(NH) 62.2118–26 (in alcohol and skins and skulls) Miri, Baram River, Sarawak, 8♂ 19♀ BM(NH) 51.88–114 (in alcohol and skins and skulls) Long Lama Caves, Baram River, Sarawak, 2♀ BM(NH) 92.9.6.24–25 (in alcohol, skulls extracted) Mt. Pisang, ♂ BM(NH) 92.9.6.26, 6♂ BM(NH) 22.10.23.1–6, 2♂ BM(NH) 58.26–7, 2♀ BM(NH) 59.155–6, ♀ BM(NH) 69.232, ♂ ♀ BM(NH) 75.1899–1900 (in alcohol and skins and skulls) Niah Cave, Sarawak, ♀ BM(NH) 92.10.2.3 (skin and skull) Mt. Dulit, BM(NH) 94.9.29.14–15, ♂ ♀ BM(NH) 78.119–120 (in alcohol, skulls extracted) Gunong Mulu, 2♂ BM(NH) 57.471–2 (in alcohol) Gomanton Caves, ♀ BM(NH) 64.38 (in alcohol) Kuching, Sarawak, ♂ ♀ BM(NH) 78.121–2 (in alcohol) Sungei Buloh, BM(NH) unregistered (in alcohol) Bidi Caves, Sarawak. MALAYA: BM(NH) 55.5.3.10 (skin and skull) Singapore, 110♂ 25♀ BM(NH) 60.1706–1840 (in alcohol, skulls extracted) Bukit Lagong Forest Reserve, Kepong, ♂ BM(NH) 61.1717 (in alcohol) Pulau Kaban, E. coast of Johore, ♂ BM(NH) 62.714 (in alcohol, skull extracted) Ulu Gombok, Selangor, ♂ ♀ BM(NH) 67.1602–3 (in alcohol and skin and skull) Gunong Benom, Pahang. RIOUW ARCHIPELAGO: 2♂ 1♀ BM(NH) 9.4.1.67–9 (skins and skulls) Karimon I. SUMATRA: ♂ BM(NH) 4.4.1.2 (in alcohol, skull extracted) Upper Langkat, Holotype of *H. schneideri* ♀ BM(NH) 7.1.9.4 (in alcohol) Soekaranda, ♀ BM(NH) 24.6.12.1 (in alcohol) Lebong Tandai, Benkalen Reserve, ♀ BM(NH) 94.1.7.5 (in alcohol, skull extracted) Engano Island, ♀ BM(NH) 95.1.9.5 (in alcohol) Simatobe, Sipora.

DIAGNOSIS. Larger on average than *H. c. cervinus*. Specimens from Malaya and Borneo have a blunt post-palatal spicule which is lacking in those from Sumatra.

Measurements of holotype: M^3–M^3 7·0; C–M^3 6·7; M^3 1·75.

Measurements of the series examined: FA (32) 43·7–51·8 (47·81); III^2 (32) 14·4–18·3 (16·58); V^2 (31) 7·8–10·5 (9·43); TL (32) 18·5–26·8 (22·7); CCL (10) 15·2–16·2 (15·78); ZW (14) 9·3–10·4 (9·91); MW (11) 9·0–9·5 (9·21); TD (12) 2·40–2·65 (2·50); M^3–M^3 (15) 6·5–7·2 (6·83); C–M^3 (16) 6·1–6·7 (6·45); M^3 (16) 1·60–1·80 (1·75).

REMARKS. Much of the confusion between *H. galeritus* and *H. cervinus* originates from Dobson (1876) who erroneously synonymized *labuanensis* with *galeritus* and who suggested (1878) that *labuanensis* was an intermediate form between *galeritus* at one extreme and *longicauda* at the other. There is every indication in the accounts by Lyon (1911), Chasen (1931, 1940) and Davis (1962) that the specimens of '*galeritus*' used in their discussions and comparisons of this species with *insolens* were actually representatives of *H. cervinus labuanensis*. Consequently, the specimens recorded by Sanborn (1952) from the Philippine Islands, should also be referred to *H. c. labuanensis* or represent a closely related taxon, since Sanborn stated that his specimens agreed with (unspecified) descriptions of *galeritus* and with Lyon's (1911) measurements.

Tate (1941) generally regarded *schneideri* as a distinct species (pp. 367, 369, 391) although he mapped it (p. 365) as a subspecies of *H. galeritus*, while Chasen (1940), Laurie & Hill

(1954) and Hill (1963) considered it a subspecies of *H. galeritus*. The Sumatran specimens examined are very similar to *H. cervinus labuanensis*, to which they are referred. Thomas (1904) separated *schneideri* from '*galeritus*' because of small differences in the premolar dentition but these appear to be the result of individual variation and are within the range of *H. cervinus*.

Medway (1958) provided a useful account of roosting and flight behaviour in Borneo which probably applies to *H. c. labuanensis*, although it is possible that his remarks refer in part to *H. galeritus insolens* since the two sometimes occur in the same caves. However, *insolens* is much less common in collections and may be solitary or live in small groups (c.f. *H. g. brachyotus*) and if so is unlikely to form part of the swarms described by Medway.

DISTRIBUTION. Malay Peninsula and Sumatra to Borneo and possibly the Philippine Islands.

Hipposideros cervinus batchianus Matschie, 1901

Hipposideros batchianus Matschie, 1901 : 273 (Batjan I.)
[Hipposideros] batchianus, Tate, 1941 : 359 (listed), 381 (holotype).
Hipposideros galeritus batchianus, Tate, 1941 : 367, 369 (systematic status), 392 (Batjan); Hill, 1963 : 56 (Batchian I. [= Batjan I.]).
Hipposideros cervinus batchianus, Tate, 1941 : 365 (mapped), Laurie & Hill, 1954 : 57 (Batchian I. [= Batjan I.]).

HOLOTYPE. In the Museum für Naturkunde der Humboldt-Universität zu Berlin. Adult ♀, number 15 628, skin and skull. Batjan Island. Not seen.

OTHER MATERIAL. None seen.

DIAGNOSIS. Measurements given by Matschie suggest that *H. c. batchianus* is similar in size to *H. c. cervinus*.

Measurements of the holotype taken from Matschie (1901): FA 47·5; III^2 12; V^2 8·5; TL 25; ZW 10; Temporal breadth from the auditory aperture 8·2; C–M^3 6·4.

DISTRIBUTION. MOLUCCA Is.: Batjan I.

Hipposideros cervinus misorensis (Peters, 1906)

Phyllorhina cervina var. *misorensis* Peters, 1906: pl. 5L, fig. 4 (probably Misor I. [= Schouten I.], New Guinea).

HOLOTYPE. Based solely on the plate by Peters, its original specimen probably in the Museum für Naturkunde der Humboldt-Universität zu Berlin, but not traceable February 1981.

OTHER MATERIAL. None seen.

REMARKS. The status of this taxon cannot be evaluated from the plate upon which it is based, beyond remarking that the noseleaf closely resembles that of *H. cervinus*, with which *misorensis* is provisionally associated.

Summary of taxonomic changes

The following taxa have been discussed and are listed below with their synonyms in brackets: *Hipposideros galeritus galeritus, H. g. brachyotus, H. g. insolens, H. g. longicaudus, H. cervinus cervinus (celebensis), H. c. labuanensis (schneideri), H. c. batchianus, H. c. misorensis.*

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